Life history and habitat associations of haddock (*Melanogrammus aeglefinus*) in Newfoundland waters

By

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A thesis submitted to the

School of Graduate Studies

In partial fulfillment of the requirements for the degree of

Master of Science

Biology

Memorial University of Newfoundland

January 2015

St. John's Newfoundland and Labrador

Abstract

Many fish stocks are currently facing collapse or overexploitation as well as warming environments. During the 1950s and 1960s, haddock supported a substantial fishery in southern Newfoundland waters, specifically Northwest Atlantic Fisheries Organization (NAFO) Divisions 3LNO and Subdivision 3Ps, but abundance has been comparatively low over the last several decades and there has been no significant fishery in either 3LNO or 3Ps since the late-1950s. The decline in the fishery for haddock coincided with a decline in scientific research on haddock with the last significant research on haddock in Newfoundland waters conducted in the 1950s-1960s. Other haddock stocks have shown major life history changes since the 1980s, including decreased size-at-age and age/length at maturity. In contrast to this, Newfoundland haddock have not shown a significant change in growth or maturity through time. Based on analysis of habitat associations, haddock abundance is expected to increase with recent warming trends as the available optimum habitat for haddock will increase.

Acknowledgments

Special thanks to those individuals at Centre for Fisheries Ecosystems Research, Fisheries and Oceans Canada, and the crew of the RV Celtic Explorer that assisted in the collection and processing of haddock samples for this study. Financial support for this project was provided by the Government of Newfoundland and Labrador through the Department of Fisheries and Aquaculture and the Research and Development Corporation (Ignite R&D Program).

Thank you to my supervisor, Dr. Sherrylynn Rowe, for allowing me the opportunity to work on such an interesting and intellectually stimulating project and to my committee members, Drs. George Rose and Joanne Morgan, for their helpful comments and support throughout.

Thank you to Stephen Smith (formerly of the Bedford Institute of Oceanography) for help with the equations used in Ch. 2 and for providing the *BIOsurvey* R package which provided the base for most of the analyses in Ch. 2.

Thank you to my family, particularly my parents and grandmother, for their unconditional support, not just in academics but in all my life choices. And thank you to the rugby community for teaching me that perseverance, patience and hard work will always payoff, you just have to keep your chin off your chest.

Table of Contents

List of Tables

List of Figures

Introduction and Overview

Haddock (*Melanogrammus aeglefinus*) is a marine demersal gadoid broadly distributed over continental shelves on both sides of the north Atlantic Ocean. In the east, haddock range from the Irish Sea, Barents Sea, North Sea, northern Baltic Sea, to the Faroe Islands, as well as around Iceland (Blacker 1971). In the west, haddock are found from Cape Cod to the southern part of the Grand Banks off Newfoundland (Blacker 1971). Haddock can reach lengths in excess of 1 m and typically mature at 23-73 cm or 2-7 years of age, depending on the location, with males maturing at smaller sizes and younger ages than females (Blacker 1971). Adult haddock are broadcast spawners, releasing eggs directly into oceanic waters and providing them with no parental care. They are thought to breed annually for several years with individual females potentially producing tens of thousands to millions of small (< 2 mm in diameter) pelagic eggs each year (Hodder 1963; Hawkins et al. 1967; Markle and Frost 1985).

At the northern edge of their distribution in the northwest Atlantic, haddock in Newfoundland waters are comprised of two stocks on the Grand Banks and St. Pierre Bank in Northwest Atlantic Fisheries Organization (NAFO) Divisions 3LNO and Subdivision 3Ps, respectively. Historic data indicates that, although haddock were abundant (Thompson 1939), a significant fishery did not develop off Newfoundland until the late 1940s (May 1964). The majority of the haddock fishery in Newfoundland waters was driven by a few large cohorts, notably 1942, 1946 and the extraordinary 1949 year classes. Landings increased rapidly to about 105,000 t in 1955 but sporadic recruitment and over-harvesting of many of the old and large fish of the virgin population, caused

landings to decline to <10,000 t per year by the mid-1960s (May 1964; DFO 2014a, 2014b). Although there was a small increase in catch during the 1980s, primarily due to a relatively strong 1981 year class, it was not sustained and local stocks have been under moratorium to directed fishing since 1993 with haddock now only taken as bycatch in other fisheries (DFO 2014a, 2014b). The decline of haddock by the 1960s made them one of the first casualties of overfishing in North America, with the population collapsing in less than 20 years (Rose 2007).

Above average water temperatures off Newfoundland and Labrador over the last several years attributable to global climate warming coupled with a warm phase of the Atlantic Multidecadal Oscillation (Colbourne et al. 2014; DFO 2014c) may have increased haddock habitat availability and improved their productivity (Hodder 1963; Fogarty et al. 2001; Rose 2005; Drinkwater 2006). With no directed fishery for haddock permitted in Newfoundland and Labrador waters at present, improved resource status could reflect a significant economic opportunity. To better understand environmental conditions at which haddock occur in Newfoundland waters and the implications for productivity of local stocks, I set out to describe habitat associations of haddock with both temperature and depth.

Concomitant with declines in abundance, many commercially exploited marine fishes have undergone significant life history changes in recent decades (Ricker 1981; Rijnsdorp 1993; Trippel et al. 1997; Olsen et al. 2004; Swain et al. 2007). For example, Neuheimer and Taggart (2010) reported marked declines in age at maturity and mature fish length-at-age since 1970 for haddock on the Scotian Shelf. Such life history changes are critically important as they impact population growth rate and, thus, recovery rate of depleted

stocks (Cole 1954; Roff 1984). Reduced age and size at maturity, as well as truncated length distributions can be anticipated to negatively influence population growth rate as a result of factors such as increased post-spawning mortality, shortened life span, and decreased fecundity (Hutchings 1999; Beverton et al. 2004; Hutchings 2005; Venturelli et al. 2009; Jørgensen and Fiksen 2010). Given that no studies of haddock in Newfoundland waters have been undertaken since the late 1970s, I examined annual stratified random bottom trawl survey data collected by Fisheries and Oceans Canada (DFO) during 1971-2013 to determine if similar changes have occurred in these stocks. Haddock off southern Newfoundland have typically exhibited slower growth and increased recruitment variability relative to their southern counterparts (May 1964), likely due to limited habitat availability imposed by cooler temperatures, specifically to crowding within deeper warmer waters along the narrow shelf slope thought to be preferred during winter (Hodder 1963).

Overall, the primary objective of this thesis is to quantify current life history characteristics and explore habitat associations for haddock in Newfoundland waters in support of sustainable management of a haddock fishery in Newfoundland waters in the future. First, basic life history data, specifically growth and maturity, will be analyzed for each stock separately to determine if changes have occurred in these characteristics through time as well as to describe potential inter-stock differences (Chapter 1). Temperature and depth preferences for haddock in Newfoundland waters will also be explored in an attempt to better predict the potential effects of increasing temperature on distribution and productivity (Chapter 2).

The final chapter of my thesis discusses the implications of my results for haddock fisheries management in the future.

Co-authorship statement

The research described in this thesis was conceived and designed by Robert Rogers in collaboration with Dr. Sherrylynn Rowe, Dr. Joanne Morgan, and Dr. George Rose. Data was provided by Fisheries and Oceans Canada via Dr. Joanne Morgan. Data was analyzed by Robert Rogers with assistance from Dr. Sherrylynn Rowe and Dr. Joanne Morgan. All manuscripts were written by and prepared by Robert Rogers, with edits and guidance from Dr. Sherrylynn Rowe, Dr. Joanne Morgan, and Dr. George Rose. A manuscript of Chapter 1 has been submitted for peer-review to Fisheries Research and a manuscript of Chapter 2 has been submitted for peer-review to the Journal of Fish Biology.

1 Lack of life history changes in two over-exploited haddock stocks

1.1 Abstract

Concomitant with declines in abundance, many commercially exploited marine fishes have undergone significant life history changes that are critically important as they impact population growth rate and, thus, recovery rate of depleted stocks. By examining data collected as part of offshore surveys conducted during 1971-2012, I evaluated whether there have been changes in growth rate and size at maturity for haddock on Grand Bank and St. Pierre Bank, two over-exploited stocks at the northern extremity of the species range in the western Atlantic Ocean. Contrary to expectation, I found no evidence for change in either growth or maturity since 1971. However, there were differences in life history characteristics between the two stocks, as well as between males and females. Although no difference in growth was observed between sexes, differences in maturation were evident with 50% of males maturing at ~40 cm and 50% of females maturing at ~48 cm. Haddock from Grand Bank were larger than haddock from St. Pierre Bank at ages 8 and 10 by 4.4% and 7.6%, respectively. I also found that haddock on Grand Bank matured at smaller sizes (length at which the probability of maturity was 50% was 38.2 cm for males and 46.3 cm for females) than those from St. Pierre Bank (42.1 cm for males and 49.9 cm for females). The haddock fishery off Newfoundland developed rapidly from 1945 but collapsed within less than two decades. Available information suggests that while fishery exploitation rates were undoubtedly high, haddock on Grand Bank and St. Pierre Bank may not have been exposed to sufficient multigenerational fishing pressure to generate decreases in growth and maturity timing as seen in other over-exploited stocks and appear to have maintained historic life history characteristics.

1.2 Introduction

Concomitant with declines in abundance, many commercially exploited marine fishes have undergone significant life history changes in recent decades (Ricker 1981; Rijnsdorp 1993; Trippel et al. 1997; Olsen et al. 2004; Swain et al. 2007). These changes have been particularly well documented for Atlantic cod (*Gadus morhua*) stocks in the northwest Atlantic. For example, the age at which the probability of maturity is 50% declined 2-3 years over the last 5-6 decades for at least five Canadian Atlantic cod populations (Morgan and Brattey 2005; Hutchings and Rangeley 2011; Mohn and Rowe 2012). Substantial reductions in size at maturity have also been evident. Amongst eastern Scotian Shelf cod, for instance, female length at maturity declined from approximately 50 cm for cohorts in the late 1950s to 35 cm in the 1990s (Mohn and Rowe 2012). Although not as well studied as Atlantic cod, haddock in some areas have demonstrated similar life history changes (Marshall and Frank 1f999; Taylor and Steffanson 1999; Baudron et al. 2011; Skjæraasen et al. 2013). Neuheimer and Taggart (2010) reported marked declines in age at maturity and mature fish length-at-age since 1970 for haddock on the Scotian Shelf. Changes to life history characteristics often coincide with prolonged periods of exploitation and may be the product of phenotypic or genetic responses to fishing (Heino and Dieckmann 2001; de Roos et al. 2006; Ghalambor et al. 2007; Conover et al. 2009). Perhaps the most common phenotypic response occurs when reductions in population density from fishing reduce competition for limited resources and thus accelerate growth amongst individuals that remain (Engelhard and Heino 2004; Georg and Heino 2004). Faster growing fish typically mature at earlier ages than slower growing fish thus affecting a phenotypic response in age at maturity (Policansky 1993; de Roos et al. 2006). Such phenotypic responses are often short-lived and quick to reverse when there is a reduction in exploitation (Georg and

Heino 2004). In contrast, exploitation of fish stocks can also generate genetic changes which tend to be slow to reverse (Ghalambor et al. 2007; Conover et al. 2009). The probability of genetic responses to exploitation is increased with both the level of fishing mortality and the number of generations exploited (Law 2000; Hard 2004; Hutchings 2005). While it can be challenging to distinguish between phenotypic and genetic responses, analyses that have controlled for potential confounding effects suggest that fisheries-induced evolution may be the most parsimonious explanation for recent life history changes in some over-exploited fish stocks (Olsen et al. 2004; Swain et al. 2007; Neuheimer and Taggart 2010). Since this fishing induced mortality differentially selects for large fish, smaller maturing fish are more likely to survive and be able to reproduce, causing their genes to be passed on and after few generations the small bodied, slower growing fish dominate the gene pool causing a shift in the genetic structure of the population and small size to become more prevalent and advantageous in the population. Such life history changes are critically important as they impact population growth rate and, thus, recovery rate of depleted stocks (Cole 1954; Roff 1984). Reduced age and size at maturity, as well as truncated length distributions can be anticipated to negatively influence population growth rate as a result of factors such as increased post-spawning mortality, shortened life span, and decreased fecundity (Hutchings 1999, 2005; Beverton et al. 2004; Venturelli et al. 2009; Jørgensen and Fiksen 2010; but see Kuparinen and Hutchings 2012).

Haddock is a marine demersal gadoid broadly distributed over continental shelves on both sides of the north Atlantic Ocean ranging from Cape Cod to the southern part of the Grand Banks off Newfoundland in the west and in the Irish Sea, Barents Sea, North Sea, northern Baltic Sea, and the Faroe Islands in the east, as well as around Iceland (Blacker 1971). They can achieve lengths in excess of 1 m and typically mature at 23-73 cm or 2-7 years of age, depending on the

location, with males maturing at smaller sizes and younger ages than females (Blacker 1971). Adult haddock are broadcast spawners, releasing eggs directly into oceanic waters and providing them with no parental care. They are thought to breed annually for several years with individual females potentially producing hundreds of thousands to millions of small (< 2 mm in diameter) pelagic eggs each year (Hodder 1963; Hawkins et al. 1967; Markle and Frost 1985). Amongst such broadcast spawners, larger, older individuals typically spawn over longer periods in the season and exhibit higher fecundity (Hodder 1963; May 1967; Hutchings and Myers 1993; Wright and Trippel 2009).

The waters off southern Newfoundland represent the northern extremity of haddock distribution in the western Atlantic Ocean. Haddock in this area comprise two distinct management units or stocks occupying Grand Bank and St. Pierre Bank in Northwest Atlantic Fishery Organization (NAFO) Divisions 3LNO and Subdivision 3Ps, respectively (Figure 1.1). Although haddock were abundant (Thompson 1939), a significant fishery did not begin off Newfoundland until the mid-1940s (May 1964). The fishery developed quickly with landings of approximately 105,000 t in 1955 but with only sporadic recruitment and having harvested many of the old and large fish of the virgin population, catch levels rapidly declined to reach low levels (<10,000 t per year) by the mid-1960s (May 1964; DFO 2014a, 2014b). There was a small increase in catch during the 1980s, primarily as a result of a relatively strong 1981 year class, but this was not sustained and local stocks have been under moratorium to directed fishing since 1993 although haddock continue to be taken as bycatch in other fisheries (DFO 2014a, 2014b).

Given the large changes in haddock life history that have occurred in nearby areas (Neuheimer and Taggart 2010) and the absence of studies on haddock in Newfoundland waters since the 1970s (Templeman et al. 1978a, 1978b; Templeman and Bishop 1979a, 1979b), the

primary objective of the current study was to examine current life history patterns and their implications for management of a potential haddock fishery in the future. Specifically, by examining data collected as part of offshore research surveys conducted during 1971-2012, growth rate and size at maturity for both the Grand Bank and St. Pierre Bank haddock stocks including potential sexual and inter-stock differences were evaluated, as well as whether there have been any shifts in these traits over time.

1.3 Materials and methods

Haddock life history characteristics in NAFO Divisions 3LNO and Subdivision 3Ps were assessed using data collected from offshore research depth-stratified random bottom trawl surveys conducted during 1971-2012 by Department of Fisheries and Oceans (DFO) Canada. NAFO Divisions 3LNO were surveyed in spring from 1971 to 2012 although there was no survey in 1983. NAFO Subdivision 3Ps was surveyed mainly in February and March from 1972 to 1992 but in April-May since 1993. Although differences in survey timing could impact perceived growth rates, no attempt was made to adjust measurements as 80% of growth takes place between August and November, outside of the winter-spring survey period (Needler 1931). During 1971-1982, surveys were conducted using the Yankee trawl which was replaced by the Engels trawl during 1983-1995, and the Campelen trawl during 1996-2012. Upon capture at sea, fork length (from the tip of the snout to the medial aspect of the caudal fin) of each individual haddock was measured to the nearest centimetre. Sex and maturity status of each individual were determined by observation of gross morphology of the gonad (Templeman et al. 1978b). For a length stratified subset of captured individuals, scales were extracted for age estimation

using standard procedures. DFO age readers were part of exchange programs to ensure that ageing is consistent over time and between readers.

1.3.1 Growth

Haddock growth was described using the organic growth equation developed by von Bertalanffy (1938)

$$L_t = L_\infty\left(1 - e^{-k[t-a_0]}\right) + \varepsilon \qquad \text{(Eq. 1)}$$

whereby length at age (L_t) is a function of maximum body length (L_∞), a growth rate coefficient that determines how fast maximum size is attained (k), and the hypothetical age that individuals have zero length (a_0; fixes curve along x-axis) (von Bertalanffy 1938). Model parameters were estimated using generalized nonlinear least squares for males and females separately in each stock and in each year for which there were data (1971-2004; aging data were not available beyond 2004). To minimize potential impacts of reduced sample sizes at older ages, growth was examined in relation to stock origin and sex, as well as over time by comparing parameter estimates as opposed to back-calculated lengths at age.

Assessing variation in growth was a multi-step process where variables were first log-transformed such that they became linear. In the case of a_0 where negative values were sometimes estimated, 10 was added to the value before log-transformation. The significance (α=0.05) of potential differences was tested using linear models. Parameters from the von Bertalanffy equation (Eq. 1) were estimated for each year for each sex separately and then with both sexes combined. Differences in relation to sex were then analyzed for all years. Specifically,

$$log\begin{pmatrix} L_\infty \\ k \\ a_0 + 10 \end{pmatrix} = \begin{pmatrix} \beta_{0L} + x_q\beta_{qL} \\ \beta_{0k} + x_q\beta_{qk} \\ \beta_{0a} + x_{iq}\beta_{qa} \end{pmatrix} \text{(Eq. 2)}$$

where β_{0L} = the intercept of the model, β_q= the regression coefficient of x_q, and x_q = the effect of either: sex, year, or sex within year. If sexual differences were not apparent, parameters were re-estimated for both sexes combined and the above analysis repeated. Inter-stock differences were also assessed using a Welch's two-sample t-test of length at age for haddock aged 2, 4, 6, 8, and 10 years in all years available.

1.3.2 Maturity

To assess potential variation in size at maturity, the length at which the probability of maturity was 50% (L50) was estimated for males and females separately in each stock by fitting a logistic model with logit link function and binomial error to the data (Trippel et al. 1997; Morgan and Colbourne 1999). Scarcity of data in some years precluded L50 from being estimated on an annual basis and so three year blocks were examined (Fig. 1.3). Temporal changes in L50 were assessed using linear modelling for each stock and inter-stock differences were assessed using Welch's two-sample t-test. All analyses were conducted using the free statistical software R (R Core Team 2014).

1.4 Results

1.4.1 Growth

Haddock encountered during DFO research vessel surveys conducted from 1971 to 2004 in NAFO 3LNO and 3Ps ranged 7-120 cm in fork length and 0-16 years in age. No sexual

differences were observed in any of the von Bertalanffy parameters for haddock in 3LNO or 3Ps (Table 1.1) and, as a result, sexes were combined and von Bertalanffy parameters re-estimated for temporal analysis (Table 1.2). Analysis of von Bertalanffy parameters estimated with both sexes combined indicated no temporal differences for either the 3LNO or 3Ps stock (Tables 1.1 and 1.2) during 1971-2004, although differences were observed between stocks. Comparisons between stocks indicated no significant differences in growth for fish aged 2 (t=-0.74, df=27.3, p=0.77), 4 (t=-0.61, df=27.6, p=0.73), and 6 (t=0.76, df=30.0, p=0.23) years, although fish aged 8 (t=2.66, df=34.1, p=0.006) and 10 (t=4.16, df=34.9, p<0.001) years were significantly different with 3LNO haddock showing a greater length at age (Table 1.3 and Fig. 1.2).

1.4.2 Maturity

For male and female haddock in NAFO Divisions 3LNO and subdivision 3Ps, L50 did not differ through time (3LNO males: p = 0.27; 3Ps males: p = 0.85; 3LNO females: p = 0.28; 3Ps females: p = 0.26; Fig. 1.3). Although no significant differences were found among years, there were significant differences in relation to sex with females exhibiting a greater L50 than males in both 3LNO (mean fork length ± 1 SE = 38.2 ± 4.1 cm for males and 46.3 ± 4.7 cm for females, $t_{19.6}$ = 4.30, p < 0.001) and 3Ps (42.1 ± 2.6 cm for males and 49.9 ± 4.6 cm for females, t16.0 = 4.84, p < 0.0001). Males in 3Ps had higher L50 than those in 3LNO (t17.1 = 2.60, p < 0.01) although there was no significant difference amongst females (t20.0 = 1.79, p = 0.09; Fig. 1.3).

1.5 Discussion

Contrary to expectation, no evidence was found for change in either growth rate or size at maturity amongst haddock from the Grand Bank or St. Pierre Bank since 1971. Given that

haddock in southern Newfoundland waters were intensely exploited in the past, why do these stocks not appear to have undergone the types of life history changes documented in other over-exploited marine fish populations?

The lack of life history change in haddock stocks off southern Newfoundland may relate to the pattern of their exploitation. Although plentiful, haddock were not heavily fished in Newfoundland waters until the 1940s (Thompson 1939; May 1964). The haddock fishery developed rapidly from 1945 but collapsed within less than two decades. Many of the old and large fish of the virgin stock were taken within the first several years and high landings were maintained until the early 1960s only as a result of strong cohorts in 1949 and 1955 (May 1964; Rose 2007). Although fishing mortality was undoubtedly high, the short duration of the fishery which would have corresponded to approximately 2-3 generations might not have been sufficiently great to effect a genetic response in life history traits (Conover et al. 2009). In addition to intense exploitation pressure, the fishery of this era was characterized by high discard rates estimated at 30-40% by weight and 50-70% by numbers because of small mesh size (70-100 mm) used and a requirement by fish plants that landed catch be at least 45 cm (May 1964; DFO 2014b). Although the fate of discarded fish is unknown, fishing mortality on this younger, immature segment of the population was also likely high (Benoît et al. 2012a; Benoît et al. 2012b). Discard rates were reduced after 1953 when Newfoundland fish plants began to accept smaller haddock measuring 33-43 cm (May 1964). Given that fishing impacted such a broad range of sizes and ages, the potential for size-selective mortality and fisheries-induced evolutionary change might have been similarly reduced. By comparison, Neuheimer and Taggart (2010) reported that, after controlling for density-dependence and temperature as contributing factors, the observed decreases in growth and maturity timing for Scotian Shelf

haddock during 1970-2008 were most likely attributable to fisheries-induced evolutionary change brought about by high fishing mortality and sustained harvesting of large fish over several decades or multiple generations. Reduced productivity and increased recruitment variability within the cold waters off Newfoundland, the northern edge of haddock distribution in the western Atlantic Ocean (Blacker 1971), likely made local haddock stocks more vulnerable to overfishing than their southern counterparts and led to their rapid demise (May 1964; Fogarty et al. 2001; Rose 2007). As a result, available information suggests that haddock on Grand Bank and St. Pierre Bank may not have been exposed to sufficient multigenerational fishing mortality to cause long-term decreases in growth and maturity, as seen in some other over-exploited stocks.

The possibility that life history changes have occurred within Grand Bank and St. Pierre Bank haddock stocks but were not detected in the present study cannot be concluded. For example, when examining Barents Sea haddock cohorts spanning 1983-2003, contrary to expectation, Devine and Heino (2011) found little evidence of a consistent trend in maturation tendencies or fisheries-induced evolution. They suggested that the lack of a significant temporal trend in maturation might have been due to challenges in estimating population parameters for the stock, the trait change being in a period of stasis or reversal, or adaptation by the fish to higher exploitation in the past resulting in negligible evolutionary selection during the study period when exploitation was more moderate (Devine and Heino 2011). Similar issues may have been at play in the present investigation given that the survey series did not extend back in time beyond 1971 and represented a period post-collapse of the haddock fishery – life history changes may have taken place but prior to the start of our data set. However, this seems to be an unlikely possibility given that growth rates and maturity measured here appear broadly similar to those

reported by Thompson (1939) who examined Newfoundland haddock when they were only lightly fished and thus essentially described an untouched or virgin stock. Thompson (1939) documented haddock measuring approximately 28, 45, and 50 cm at ages 2, 4, and 6 years, respectively. Our data are also consistent with observations of haddock off Newfoundland during the late 1940s to late 1960s (Templeman et al. 1978a; Templeman and Bishop 1979b) although given differences in sampling methodology, some caution is warranted in drawing these comparisons. Hodder (1962) described reduced growth of haddock off Newfoundland from the late 1940s to mid-1950s with fish measuring 25, 36, and 43 cm at ages 2, 4, and 6, respectively. An additional possibility is that changes in life history characteristics occurred in response to early fishing activities but subsequently reversed before the start of the survey series in 1971. While this scenario cannot be entirely discounted, it does not appear probable given that available information for these stocks generally shows similar life history characteristics over time (Thompson 1939; Templeman et al. 1978a; Templeman and Bishop 1979b; present study) and that reversal of 'evolutionary downsizing' caused by fishing is a process anticipated to take decades (Conover et al. 2009). Reduced growth observed by Hodder (1962) was most likely attributable to density-dependent effects resulting from the large increases in abundance of haddock in both stocks due to the extraordinary 1949 year class and its offspring.

An additional aspect of this research was to assess potential sexual and inter-stock variation in haddock growth and maturity. Consistent with other studies, the present study found that male haddock typically matured at smaller sizes than females (Blacker 1971). Sexual differences in maturity schedules are not uncommon amongst fishes and may relate to life history tradeoffs (Andersson 1994). Grand Bank and St. Pierre Bank haddock stocks are managed as independent groups (DFO 2014a, 2014b) and intermingling of adult haddock between these areas is thought

to be limited by hydrographic barriers, particularly a moderately deep channel present between Green Bank and Grand Bank that, along with Green Bank itself, features water temperatures generally lower than those preferred by haddock (May 1964; Rogers et al. submitted). As anticipated, there was some evidence for inter-stock life history differences that may be attributable to either genetic variability between stocks or phenotypic responses to the differing environmental conditions in these areas (Colbourne et al. 2014; Rogers et al. submitted). Close spatial proximity of these two stocks makes genetic differences seem unlikely given the potential for drift of eggs and larvae. Hodder (1966) noted "…haddock were not known to exist in abundance on St. Pierre Bank prior to 1950…the water current pattern, immediately following the Grand Bank spawning in 1949, was such that haddock larvae in great numbers drifted in the general direction of St. Pierre Bank…the population subsequently developing its own distinctive growth characteristics". Additionally, Rogers et al. (submitted) found that although haddock in both Newfoundland stocks occupied similar temperatures, environmental conditions vary greatly between these management areas lending support to the notion that observed inter-stock life history differences may be phenotypically based. Although molecular genetic work supports the existence of discrete stocks of haddock within the northwest Atlantic (Zwanenburg et al. 1992), the author is not aware of any studies that have applied this approach to haddock on both Grand Bank and St. Pierre Bank.

1.6 Conclusions

Examination of life history characteristics revealed no evidence for change in growth and maturity amongst Newfoundland haddock stocks during 1971-2012. This lack of change may relate to the pattern of exploitation of these stocks, particularly the brief duration of the fishery

271 which potentially resulted in insufficient multigenerational fishing pressure. Inter-stock
272 differences in growth and maturity were evident however and support the management of these
273 stocks as separate units.
274 Should a directed fishery for haddock resume off Newfoundland in the future, further
275 research into recruitment and survival dynamics will be critical to establish management
276 strategies that recognize local rates of productivity.
277
278

1.6 Tables

Table 1.1 Parameter estimates from linear modeling von Bertalanffy growth parameters for haddock in NAFO Divisions 3LNO and Subdivision 3Ps. Note that male and female haddock were pooled for analysis of annual differences (Year). See methods (2.1) for details. L_∞ = asymptotic length, k = growth rate, a_0 = theoretical age at which fish measure 0 cm in length.

			Estimate[1]	t-value (d.f.)	*p*-value
Sex	3LNO	$\beta_{L\infty}$	0.004	0.169 (32)	0.87
		β_k	-0.002	-0.050 (32)	0.96
		β_{a0+10}	0.002	0.361 (32)	0.72
	3Ps	$\beta_{L\infty}$	-0.038	1.70 (37)	0.10
		β_k	-0.046	-1.15 (37)	0.26
		β_{a0+10}	-2.80E-4	-0.065 (37)	0.95
Year	3LNO	$\beta_{L\infty}$	0.003	0.370 (17)	0.72
		β_k	-0.008	-0.529 (17)	0.60
		β_{a0+10}	-6.20E-4	-0.282 (17)	0.55
	3Ps	$\beta_{L\infty}$	1.41E-2	1.66 (19)	0.11
		β_k	2.31E-2	-1.78 (19)	0.09
		β_{a0+10}	0.000	-0.605 (19)	0.76

[1]Estimates are log transformed

288 **Table 1.2** Parameter estimates as calculated from the von Bertalanffy equation (Eq. 1) for
289 haddock in NAFO Divisions 3LNO and Subdivision 3Ps (sexes combined). Missing values
290 resulted from insufficient data. L_∞= asymptotic length, k= growth rate, a_0= theoretical age at
291 which fish measure 0 cm in length. Years with missing data are due to insufficient fish being
292 sampled in that year to fit a von Bertalanffy curve.

293

	3LNO			3Ps		
Year	L_∞	k	a_0	L_∞	k	a_0
1971	92.07	0.22	0.08	--	--	--
1972	--	--	--	71.16	0.24	-0.09
1973	124.78	0.13	-0.02	88.51	0.17	-0.36
1974	--	--	--	79.97	0.22	-0.4
1975	166.25	0.074	-0.92	--	--	--
1976	--	--	--	107.34	0.13	-0.46
1977	--	--	--	103.1	0.15	-0.14
1979	--	--	--	111.28	0.13	-0.29
1980	84.65	0.22	-0.23	84.11	0.22	-0.13
1981	--	--	--	88.98	0.17	-0.31
1982	117.98	0.11	-0.50	--	--	--
1983	--	--	--	107.28	0.13	-0.54
1984	121.46	0.09	-0.81	--	0.05	-1.11
1985	159.64	0.06	-0.91	103.18	0.13	-0.46
1986	183.44	0.05	-0.44	95.21	0.16	-0.23
1987	194.91	0.05	-0.72	103.82	0.12	-0.46

1988	190.45	0.05	-1.11	--	0.07	-0.59
1989	211.24	0.05	-0.64	105.26	0.12	-0.51
1990	--	--	--	97.03	0.18	0.04
1992	--	--	--	--	0.06	-0.67
1993	--	--	--	--	0.04	-0.58
1995	--	--	--	93.52	0.17	0.16
1996	293.71	0.03	-1.99	99.79	0.15	-0.18
1997	86.94	0.24	0.85	92.95	0.16	-0.16
1998	113.34	0.13	-0.38	96.04	0.18	0.05
1999	112.06	0.12	-0.69	--	0.04	-1.48
2000	145.38	0.07	-1.15	--	--	--
2001	114.02	0.13	-0.12	--	--	--
2003	130.38	0.11	0.16	--	--	--
2004	140.5	0.08	-0.66	--	--	--

294

295

296 **Table 1.3** Mean fork length of haddock aged 2, 4, 6, 8, and 10 years in NAFO Divisions 3LNO
297 and Subdivision 3Ps during 1971-2004.

298

Age	Mean fork length (SE)		t-value (d.f.)	*p*-value
	3LNO	3Ps		
2	28.0 (3.3)	28.6 (1.7)	-0.74 (27.4)	0.46
4	46.1 (3.9)	46.7 (2.0)	0.61 (27.6)	0.55
6	60.7 (4.1)	59.8 (2.5)	0.76 (30.0)	0.45
8	72.5 (4.0)	69.4 (3.2)	2.66 (34.1)	<0.01
10	82.3 (4.6)	76.3 (4.2)	4.16 (34.9)	<0.0001

299

1.7 Figures

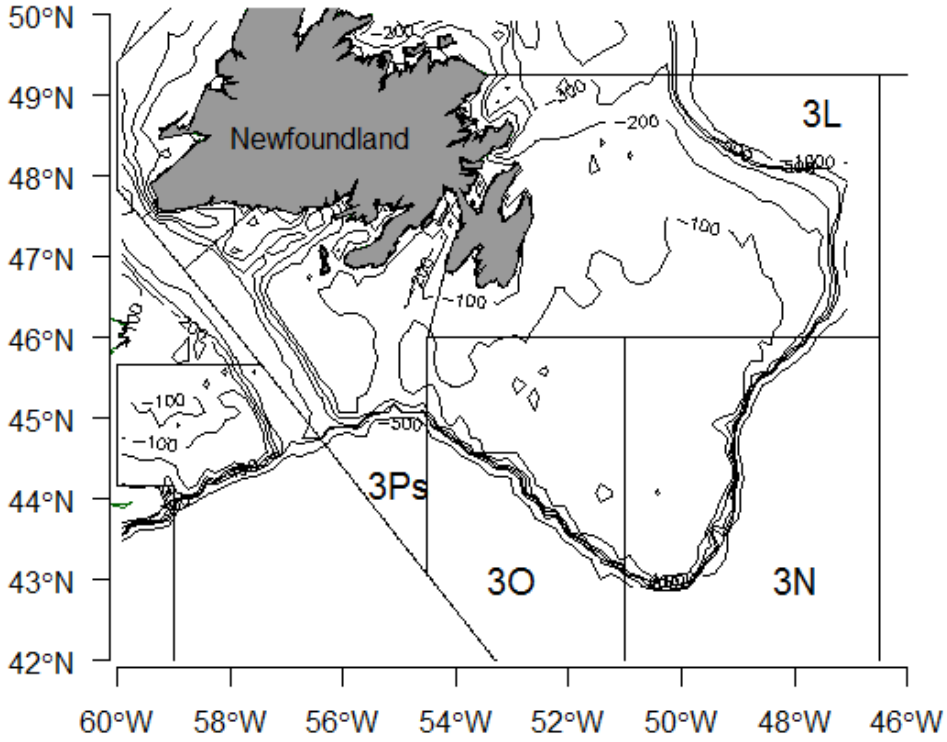
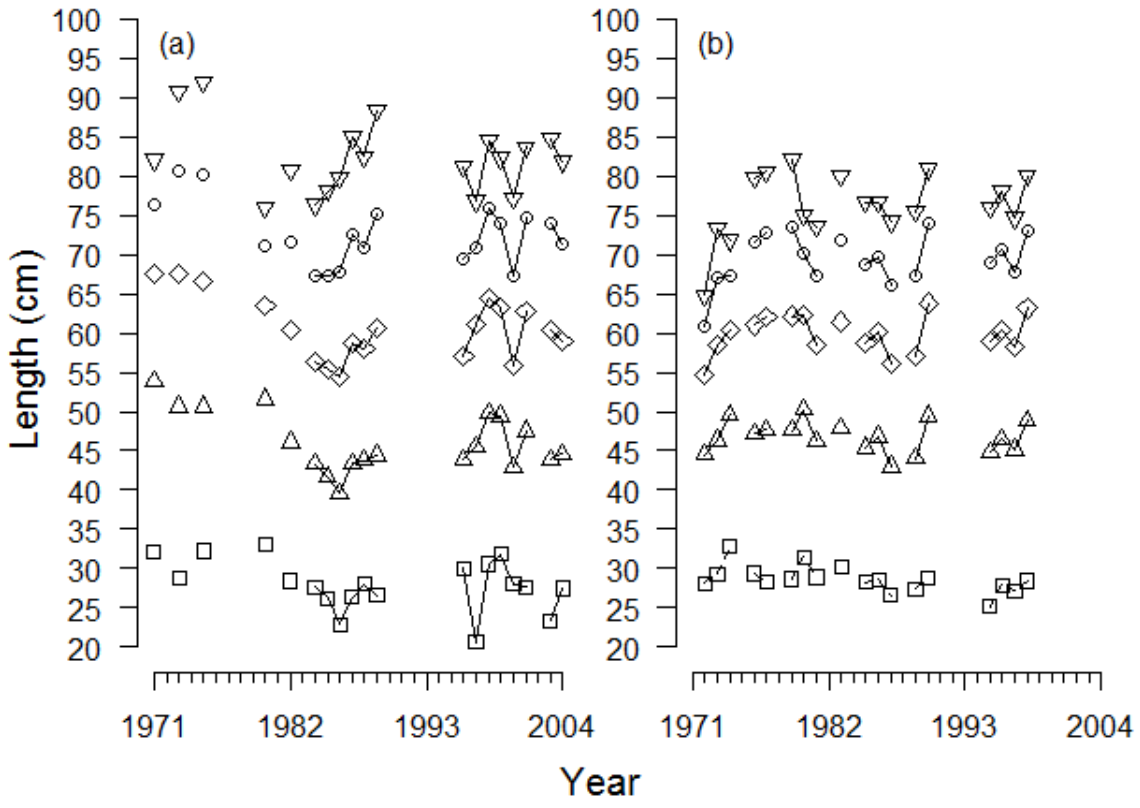


Figure 1.1 Waters off Newfoundland showing NAFO Divisions and depth contours.



304

305 **Figure 1.2** Annual haddock length at age in NAFO Divisions 3LNO (a) and Subdivision 3Ps (b)
306 predicted based on parameters estimated using non-linear least squares regression. Squares,
307 triangles, diamonds, circles, and inverted triangles represent haddock aged 2, 4, 6, 8, and 10
308 years, respectively.

309

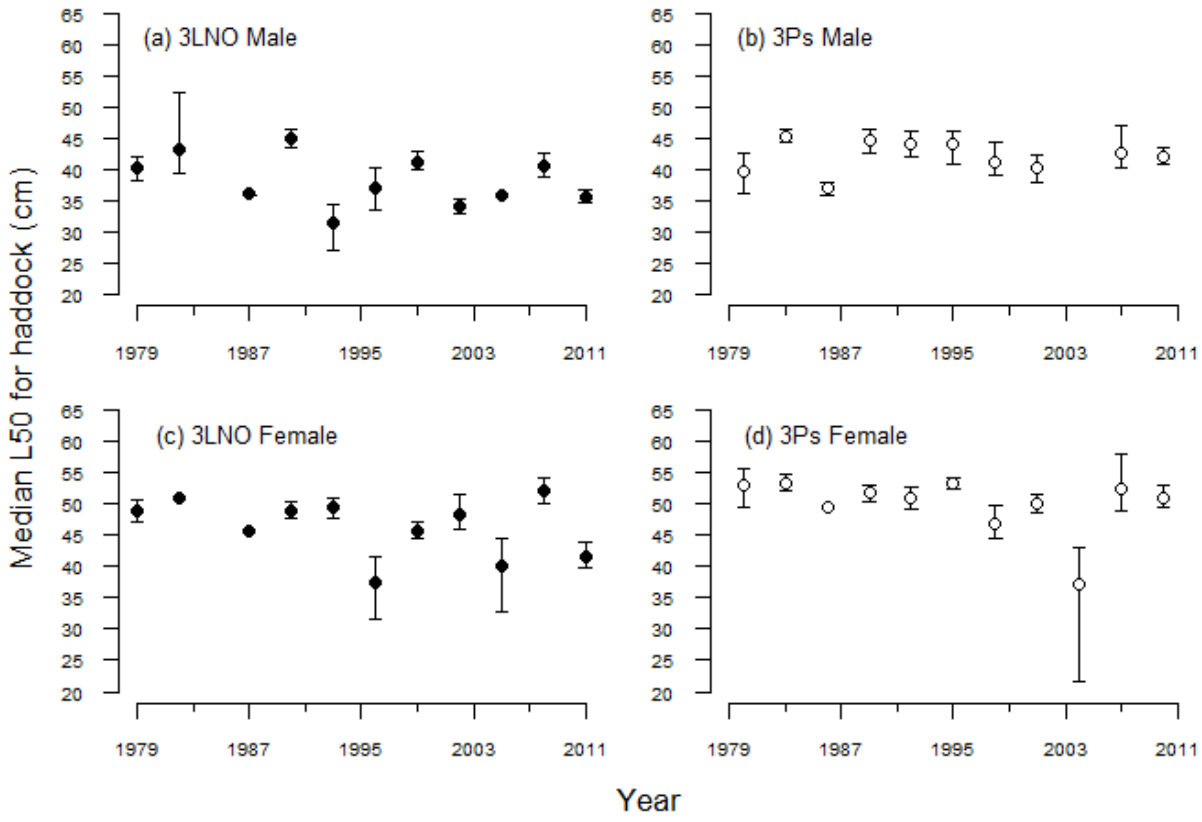


Figure 1.3 Mean length at 50% maturity with 95% confidence intervals for 3LNO male (a), 3Ps male (b), 3LNO female (c), and 3Ps female (d) haddock using three year groupings. Points represent the median year of each group.

2 Depth and temperature associations of haddock (*Melanogrammus aeglefinus*) off southern Newfoundland

2.1 Abstract

Knowledge of the environmental conditions at which fish occur can be instrumental in improving survey design and abundance estimation, highlighting important areas for critical life history stages, as well as understanding and predicting environmental influences on fish distribution and migration patterns. Using data collected as part of offshore surveys conducted during 1972-2013, I quantified haddock association patterns with depth and temperature in southern Newfoundland waters, the northern extremity of the species' range in the western Atlantic Ocean. Our results showed that haddock were typically concentrated in the deep warm waters along the narrow shelf slope in Northwest Atlantic Fisheries Organization (NAFO) Divisions 3O and 3P with individuals moving seasonally into the shallow waters of the banks as they warmed. While haddock were found over a range of depths and temperatures, they were primarily located at depths deeper and temperatures warmer than the median sampled. Analyses demonstrated that of the two habitat variables assessed, temperature was most influential in structuring haddock distribution with individuals appearing to change depth in order to maintain similar temperature throughout the year. Haddock were found predominantly in temperatures of approximately 4-7 °C which often represented some of the warmest waters available. Differences in fish-habitat association patterns in relation to sex or maturity status were not readily apparent from our analyses. Warming conditions off Newfoundland and Labrador in recent years might be predicted to improve local haddock productivity.

2.2 Introduction

Fish are not randomly distributed within their environment but rather typically concentrated in areas with particular hydrographic features such as depth, temperature, or salinity (Scott 1982; Murawski and Finn 1988; Perry and Smith 1994). Habitat associations may be strong and can vary amongst populations (Perry and Smith 1994; Smith and Page 1996) and seasons (Clark and Green 1991; Swain et al. 1998), as well as between sexes (Shepherd et al. 2002). Physiological needs may directly drive some habitat associations. For example, as ectotherms with the rate of physiological processes regulated by ambient temperature (Fry 1971; Atkinson 1994), many fish might be expected to seek particular thermal environments during certain periods, such as when females are readying oocytes to spawn (Murawski and Finn 1988; Page and Frank 1989; Swain et al. 1998). Depth associations have been documented for many species (e.g., Scott (1982); Perry and Smith (1994); Swain et al. (1998); Shepherd et al. (2002) although these might actually represent preferences for certain correlated temperatures, prey availability, or sediment types (Perry and Smith 1994; Swain et al. 1998). Knowledge of the environmental conditions in which fish occur is critical to understanding environmental influences on fish distribution and migration patterns (Rose and Leggett 1988) and can also lead to improved survey design and abundance estimation (Smith 1990). Analyses of fish habitat associations may also highlight important areas for critical life history stages that could be used to guide practices within an ecosystem-based approach to fisheries management such as the protection of spawning grounds (Gavaris 2009).

Haddock (*Melanogrammus aeglefinus*) is a commercially valuable demersal gadoid distributed from Cape Cod to the southern part of the Grand Banks off Newfoundland in the western Atlantic Ocean and in the Irish Sea, Barents Sea, North Sea, northern Baltic Sea, and the

Faroe Islands in the eastern Atlantic Ocean, as well as around Iceland (Blacker 1971). Haddock inhabit inshore regions to the edge of the continental shelf and can exhibit marked seasonal differences in depth distribution typically overwintering in deeper waters and moving into shallower areas as they warm in summer (Scott and Scott 1988). Accordingly, on the Scotian Shelf, they have been characterized as 'temperature-keepers', changing their depth distribution to maintain similar temperature throughout the year (Perry and Smith 1994). However, this behaviour may be more pronounced in cooler parts of the species distribution as haddock in more temperate areas such as Georges Bank have been reported to maintain similar depths among seasons (Murawski and Finn 1988).

The waters off southern Newfoundland represent the northern extremity of haddock distribution in the western Atlantic Ocean. Haddock in this area comprise two distinct stocks occupying Grand Bank and St. Pierre Bank in Northwest Atlantic Fisheries Organization (NAFO) Divisions 3LNO and Subdivision 3Ps, respectively (Figure 2.1). Historical records indicate that although haddock were abundant (Thompson 1939), a significant fishery did not develop off Newfoundland until the late 1940s (May 1964). Landings increased rapidly to a peak of approximately 105,000 t in 1955 but with only sporadic recruitment and having harvested many of the old and large fish of the virgin population, declined to <10,000 t per year by the mid-1960s (May 1964; DFO 2014a, 2014b). Although there was a small increase in catch during the 1980s, primarily due to a relatively strong 1981 year class, it was not sustained and local stocks have been under moratorium to directed fishing since 1993 with haddock now only taken as bycatch in other fisheries (DFO 2014a, 2014b). Haddock off southern Newfoundland have typically exhibited slower growth and increased recruitment variability relative to their southern counterparts (May 1964). Reduced productivity of haddock in this area may relate to

limited habitat availability imposed by cooler temperatures, specifically to crowding within deeper warmer waters along the narrow shelf slope thought to be preferred during winter (Hodder 1963). Above average water temperatures off Newfoundland and Labrador over the last several years attributable to global climate warming coupled with a warm phase of the Atlantic Multidecadal Oscillation (Colbourne et al. 2014; DFO 2014c) may have increased haddock habitat availability and improved their productivity (Hodder 1963; Fogarty et al. 2001; Rose 2005; Drinkwater 2006). With no directed fishery for haddock permitted in Newfoundland and Labrador waters at present, improved resource status could reflect a significant economic opportunity.

To better understand the environmental conditions at which haddock occur in Newfoundland waters and potential implications for productivity of local stocks, I set out to describe haddock association patterns with depth and temperature. Specifically, by examining data collected as part of offshore surveys conducted during 1972-2013, I quantified habitat associations for both the Grand Bank and St. Pierre Bank haddock stocks and assessed whether they have shifted over time or varied between stocks. Because haddock in some areas are known to make seasonal migrations (Scott and Scott 1988), I also investigated potential seasonal differences in habitat associations. Similarly, I explored potential differences in habitat associations in relation to sex and maturity status.

2.3 Materials and methods

Haddock habitat associations in NAFO Divisions 3LNOP were assessed using data collected from offshore research depth-stratified random bottom trawl surveys conducted during 1972-2013 by Department of Fisheries and Oceans (DFO) Canada. Years surveyed and survey timing varied amongst areas. Spring surveys were conducted in NAFO Divisions 3LNO during 1975-

2013 (although there was no survey in 1983). Fall surveys were conducted in NAFO Division 3L during 1981-2013 and in Divisions 3NO during 1990-2013. NAFO Division 3P was surveyed mainly in February and March (winter) from 1972 to 1992 but in April-May (spring) since 1993. Given that the survey is conducted for 3P as a whole, I examined haddock distribution over all of NAFO Division 3P although for management purposes, the stock is delineated as NAFO Subdivision 3Ps. During 1972-1982, surveys were conducted using the Yankee trawl which was replaced by the Engel trawl from 1983 to spring 1995, and the Campelen trawl from fall 1995 to 2013. While the survey design has remained constant, new strata have been added since 1993 and some of the original strata modified (Doubleday 1981; Bishop 1994). Haddock habitat associations were quantified annually for each NAFO Division and season. Because of changes to stratification scheme and gear type, analyses that involved examination of data over multiple years were blocked into temporal periods of comparable survey methodology. For example, in NAFO Division 3O, four strata were modified and deep-water strata added in 1994 and the Campelen trawl was introduced in fall 1995 thus necessitating that data for fall surveys would be blocked as pre-1994, 1994, and 1995-2013. The Yankee and Engel trawls are thought to be relatively similar in selectivity allowing data from these gears to be combined but differ substantially from the Campelen trawl which is more effective at catching smaller fish and invertebrates (McCallum and Walsh 1996). The survey sample unit was defined as the bottom area fished (i.e., swept area) during a standard tow at constant speed (3.5 nm/hour for Yankee/Engel and 3.0 nm/hour for Campelen) – 0.01332 nm^2 for a standard 30 minute tow using the Yankee or Engel trawl and 0.00727 nm^2 for a standard 15 minute tow using the Campelen trawl. As a result, I were unable to resolve fish-habitat associations at a scale finer than the area of a survey tow. For each set, the total number and weight of haddock captured

was recorded. In addition, for each individual haddock, fork length (from the tip of the snout to the medial aspect of the caudal fin) was measured to the nearest centimetre and sex and maturity status determined by observation of gross morphology of the gonad (Templeman et al. 1978b). Bottom temperature at the set location was quantified using a mechanical or expendable bathythermograph (MBT or XBT, respectively) during 1972-1988 and a trawl mounted conductivity, temperature, and depth (CTD) logger during 1989-2013. Bottom depth was obtained using the ship's echo sounder (Morgan and Colbourne 1999).

2.3.1 Univariate habitat associations

Although many techniques exist for the quantification of fish habitat associations, I opted to use the approach outlined by Perry and Smith (1994). While computationally complex, this method involving cumulative distribution functions (CDFs) and randomization testing offers several advantages insofar as it accounts for survey design and available habitat conditions and does not require any assumptions to be made in relation to statistical distribution of either fish catch or habitat variables (Perry and Smith 1994). The later point is particularly relevant as standard parametric or nonparametric tests can give erroneous results when applied to data derived from complex survey designs (Rao and Thomas 1989).

Identifying associations between haddock catch and environmental data from the surveys was a three-step process. First, I constructed the CDF of each habitat variable (depth and temperature) while incorporating the survey design as

$$f(t) = \sum_h \sum_i \frac{W_h}{n_h} I(x_{hi}) \qquad \text{(Eq. 1; Perry and Smith (1994)}$$

with the indicator function

$$I(x_{hi}) = \begin{cases} 1, & \text{if } x_{hi} \leq t; \\ 0, & \text{otherwise.} \end{cases}$$

where W_h = proportion of the survey area in stratum h, n_h = number of sets in stratum h, x_{hi} = measurement of hydrographic variable in set i of stratum h, and t = index ranging from the lowest to the highest value of the habitat variable at a step size appropriate for the desired resolution. Inclusion of terms (W_h/n_h) to describe the stratification scheme ensured that the estimate of the frequency distribution for the habitat variable was unbiased (Perry and Smith 1994).

The second step was to calculate the catch-weighted CDF to associate the number of haddock in each set with the habitat conditions at that set

$$g(t) = \sum_h \sum_i \frac{W_h}{n_h} \frac{y_{hi}}{y_{st}} I(x_{hi}) \qquad \text{(Eq. 2; Perry and Smith (1994)}$$

where y_{hi} = number of haddock caught in set i and stratum h and y_{st} = estimated stratified mean abundance of haddock calculated using

$$y_{st} = \sum_{h=1}^{L} W_h y_h \qquad \text{(Eq. 3; Smith (1990, 1997)}$$

where y_h = estimated mean abundance of haddock in stratum h ($y_h = \sum_{i=1}^{n_h} y_{hi}/n_h$; Smith (1990, 1997).

The third, and final, step was to determine the strength of the association between the habitat variable and haddock catch by comparing the habitat available curve (*f(t)*) with the habitat used curve (*g(t)*) and finding the maximum absolute vertical difference between them (*D*; Figure 2.2) where

$$D = \max|g(t) - f(t)|$$

$$= \max\left|\sum_h \sum_i \frac{W_h}{n_h}\left(\frac{y_{hi} - y_{st}}{y_{st}}\right) I(x_{hi})\right| \qquad \text{(Eq. 4; Perry and Smith (1994)}$$

474 *D* was the test statistic used to determine whether or not the association between habitat and
475 haddock catch was significant and is essentially the Kolmogorov-Smirnov test statistic (Conover
476 1980). However, random stratified survey design complicates assumptions about distribution of
477 the test statistic so that standard tables for the Kolmogorov-Smirnov test cannot be used (Rao
478 and Thomas 1989; Perry and Smith 1994). Perry and Smith (1994) developed a randomization
479 procedure in which they modelled the distribution of the test statistic under the null hypothesis of
480 random association between habitat and fish catch using Monte-Carlo simulation. This approach
481 was employed here and involved randomizing pairings of $(W_h/n_h)[(y_{hi}-y_{st})/y_{st}]$ and x_{hi} for all *h* and
482 *i* within the survey and then calculating the test statistic for those pairs (Eq. 4; (Perry and Smith
483 1994). The procedure was repeated *K* times to establish a pseudo-population (*D'*) of test
484 statistics under the null hypothesis. Significance levels were assessed using the formula for
485 Kolmogorov-Smirnov tests

486 $$p = \frac{\sum D' \geq D}{K+1} \qquad \text{(Eq. 5)}$$

487 where *D'* = maximum vertical difference between the randomized curves and *K* = number of
488 times resampling occurred (*K*+1 was used to account for the original *D*).

489 *2.3.2 Influences of sex and maturity on habitat associations*

490 To determine whether habitat associations varied in relation to sex or maturity, habitat
491 associations of each grouping (immature female, immature male, mature female, mature male)
492 were quantified by applying the proportion of each grouping in each particular set to the total
493 number of haddock caught in the catch. These numbers then served as the 'population' (*g(t)*)
494 being examined, as per Eq. 2. Assessing whether differences between groups were significant
495 was accomplished in a process similar to Eq. 4 although with some modification. In particular,

the method was altered such that each cumulative distribution curve calculated from the data (now referred to as the 'original curve') was resampled for randomized pairings of $[(W_h/n_h)*((y_{hi}-y_{st})/y_{st})]$ and x_{hi} for each h and i, a total of K times. These new curves (referred to as 'randomized curves') were then compared and the maximum vertical distance calculated in a similar fashion to Eq. 4. For example, the maximum distance between male randomized curve 1 and female randomized curve 1 was D'_1, the maximum distance between male randomized curve 2 and female randomized curve 2 was D'_2 … and the maximum distance between male randomized curve K and female randomized curve K was D'_K. Maximum distances (D') could then be used to determine whether the difference between curves was significant using Eq. 5.

2.3.3 Bivariate habitat associations

Hydrographic variables are often strongly correlated which means that an association between a species and a particular environmental variable may be confounded by an association with another environmental variable when examining variables independently. To address this potential issue, I used the methodology proposed by Perry and Smith (1994) to examine depth and temperature simultaneously. Specifically, equations 1 and 2 were modified to accommodate two or more (k) variables such that

$$f(\boldsymbol{t}) = \sum_h \sum_i \frac{W_h}{n_h} I(\boldsymbol{x}_{hi}) \qquad \text{(Eq. 6; Perry and Smith (1994)}$$

$$g(\boldsymbol{t}) = \sum_h \sum_i \frac{W_h}{n_h} \frac{y_{hi}}{y_{st}} I(\boldsymbol{x}_{hi}) \qquad \text{(Eq. 7; Perry and Smith (1994)}$$

with the indicator function

$$I(\boldsymbol{x}_{hi}) = \begin{cases} 1, & \text{if } \boldsymbol{x}_{hi1} \le \boldsymbol{t}_1, \boldsymbol{x}_{hi2} \le \boldsymbol{t}_2, \ldots \boldsymbol{x}_{hik} \le \boldsymbol{t}_k; \\ 0, & \text{otherwise.} \end{cases}$$

where all equations were as above but boldface $\boldsymbol{t}$ and $\boldsymbol{x}$ represent vectors of habitat variables. In the case of two variables, $f(\boldsymbol{t})$ and $g(\boldsymbol{t})$ can be represented as three-dimensional surfaces where the cumulative frequency forms the vertical axis (Figure 2.3). The test statistic (D) was also modified as

$$D_{bivariate} = \max|g(\boldsymbol{t}) - f(\boldsymbol{t})|$$

$$= \max\left|\sum_h \sum_i \frac{W_h}{n_h}\left(\frac{y_{hi}-y_{st}}{y_{st}}\right) I(\boldsymbol{x}_{hi})\right| \qquad \text{(Eq. 8; Perry and Smith (1994)}$$

where, again, all equations were as above but boldface $\boldsymbol{t}$ and $\boldsymbol{x}$ represent vectors of habitat variables.

To better assess the thermal habitat available to haddock over time, the design weighted area was calculated for ranges of bottom temperatures measured as part of annual winter/spring bottom trawl surveys in each NAFO Division. Area of occupancy (A) was calculated for each set (i) in each year (Y) and NAFO Division (N)

$$A_{Y,N} = \sum_{i=1}^{n} a_{i,Y,N} I$$

$$\text{where } I = \begin{cases} 1, \text{if } T_U > T_{i,Y,N} \geq T_L; \\ 0, \quad \text{otherwise.} \end{cases} \qquad \text{(Eq. 9; modified from Smedbol et al. (2002)}$$

where n = number of tows in survey in year Y and NAFO Division N, $T_{i,Y,N}$ = the bottom temperature recorded for set i in year Y and NAFO Division N, T_U = upper limit of temperature bin, T_L = lower limit of temperature bin ,and $a_{i,Y,N}$ = the area of the stratum in which tow i occurred divided by the number of sets fished in that stratum (Smedbol et al. 2002).

All analyses were undertaken in R (R Core Team 2014).

2.4 Results

2.4.1 Univariate habitat associations

Environmental conditions varied greatly amongst the survey areas (Figure 2.1; Table 2.1). Bottom depths of survey sets ranged from 20 m for inshore sets in NAFO Division 3L to >1500 m beyond the continental slope. Within NAFO Divisions 3NO, the continental shelf comprised southern Grand Bank characterized by shallow waters (typically <100 m) across the top and a steep slope along the bank edge. Bathymetry in NAFO Divisions 3L and 3P was more complex with the continental shelf including both shallow banks and deep channels with water depths measuring >200 m. Bottom temperature at survey set locations ranged -1.7-14.6 °C. Warmest temperatures were typically found in the deep waters of the narrow shelf slope, particularly in NAFO Divisions 3O and 3P, with cooler waters that warmed seasonally located on top of the shallow banks (Figure 2.1b and 1d; Table 2.1). Analysis of the thermal habitat available over time (i.e., the bottom area covered by varying range of temperature) showed warming across all areas in recent years (Figure 2.4).

Spatial and temporal variation in haddock distribution was apparent in the survey data. During winter/spring surveys, haddock were located primarily in NAFO Divisions 3O and 3P, along the narrow shelf slope (Figure 2.1a). Fall surveys of NAFO Divisions 3LNO revealed that haddock continued to be concentrated in NAFO Division 3O but could also be found in relatively high numbers within NAFO Division 3N (Figure 2.1c). During fall, haddock were found both along the shelf slope and increasingly within the shallow waters of the banks, such as on Southeast Shoal in NAFO Division 3N where temperatures warmed to approximately 6-8 °C seasonally (Figure 2.1b and 1d). Very few haddock were encountered during 1975-2013 surveys

of NAFO Division 3L (Figure 2.1a and 1c), the coldest area examined (Figure 2.1b, 1d, and 6), which prevented detailed evaluation of habitat associations within this NAFO Division.

Haddock showed wide variation in median depth used although they were often distributed at depths deeper than the median available (Figure 2.2a and 4; Table 2.1). The test statistic indicated strong associations with depth primarily in NAFO Division 3O and during the winter survey of NAFO Division 3P where values were significant ($p \leq 0.05$) in approximately 60-70% of years for each survey time series (Table 2.2). Average median depth used by haddock ranged from 65 m for individuals in NAFO Division 3N during fall to 214 m for those in NAFO Division 3P during winter (Table 2.1). Typically, median depths used by haddock have been shallower since the mid to late 1990s than in the preceding years (Figure 2.5).

Haddock were usually captured at temperatures warmer than the median available (Figure 2.2b and 5; Table 2.1) with the test statistic showing significant associations in 38-87% of years in each survey series (Table 2.2). Average median temperature used by haddock ranged from 3.0 °C for individuals in NAFO Division 3N during spring to 5.5 °C for those in NAFO Division 3P during spring (Table 2.1). While temperatures occupied by haddock often represented some of the warmest waters available, this was not the case during most recent surveys of NAFO Divisions 3O and 3P where haddock generally maintained median temperatures of approximately 4-7 °C despite warmer water available (Figure 2.6). For example, 1990 represented one of the coldest years measured on the Newfoundland and Labrador Shelf (Figure 2.4; (Colbourne et al. 2014) and haddock were observed to occupy the warmest available temperatures (~6 °C; Figure 2.2), usually found in deep water (Figure 2.7a and 7c). In contrast, 2011 was one of the warmest years measured with temperature reaching 10 °C in this area and haddock continued to occupy maximum temperatures of ~7.5 °C (Figure 2.2b) , , now available

over a broader range of depths (Figure 2.7b and 7d). Interannual variability in temperature poses a challenge for distinguishing between absolute and relative associations with particular conditions although species exhibiting absolute associations ought to display less variability among years than the variability of the habitat parameter itself (Perry and Smith 1994). Haddock appeared to demonstrate such absolute associations with particular thermal conditions in all seasonal survey series as median temperature used by haddock was less variable than the median temperature available (see relative error column of Table 2.1).

2.4.2 Influences of sex and maturity on habitat associations

Haddock did not exhibit significant habitat association differences in relation to sex or maturity status for either depth or temperature with the exception of individuals captured during winter surveys of NAFO Division 3P (Table 2.3 and Table 2.4). In this instance, significant differences were found between immature and mature males for both depth and temperature with immature individuals tending to occupy shallower and colder habitats than mature fish.

2.4.3 Bivariate habitat associations

Consistent with univariate analyses, bivariate CDF surfaces demonstrated that haddock were typically distributed over a narrow range of depths and temperatures, usually occupying areas deeper than ~130 m and warmer than 4 °C as indicated by the large increase in bivariate CDFs at these points (Figure 2.3). The test statistic (D) indicated that haddock were significantly associated ($p \leq 0.05$) with particular combined ranges of depth and temperature in approximately 14-65% of years for each survey time series (Table 2.5). To assess whether depth or temperature was most important in determining haddock distribution, I compared test results from univariate (Eq. 4) and bivariate (Eq. 8) analyses under the assumption that the variable with the strongest

association was that for which the coordinates of the test statistic changed the least between univariate and bivariate tests (Perry and Smith 1994). These analyses revealed that in most cases, the temperature at which *D* occurred changed less between univariate and bivariate cases than depth (Table 2.6). Accordingly, it appeared that when depth habitat associations were significant in the univariate case, they may have actually been driven by temperature (Table 2.6). For example, haddock in NAFO Division 3O during spring 1976 showed significant associations to both depth and temperature. However, depth at *D* changed from 91 m in the univariate analysis to 362 m in the bivariate analysis while temperature at *D* remained constant at 7.1 °C in both instances. Overall, haddock in Newfoundland waters seemed more strongly associated with certain temperatures than depths. Habitat association differences in relation to sex and maturity status were not apparent from the univariate analyses (with the exception of winter surveys of NAFO Division 3P) so bivariate analyses were not undertaken on those data.

2.5 Discussion

The goal of the present study was to examine haddock association patterns with depth and temperature in southern Newfoundland waters to improve our understanding of the environmental conditions at which haddock occur and potential implications for productivity of local stocks. Using data collected during 1972-2013, I found that haddock were typically concentrated in the deep warm waters along the narrow shelf slope in NAFO Divisions 3O and 3P with individuals moving seasonally into the shallow waters of the banks as they warmed. This distribution pattern is broadly similar to that documented for haddock prior to and during the intense fishery of the 1950s and 1960s (Thompson 1939; May 1964) although in contrast to these earlier studies which reported large quantities of haddock taken occasionally along the east coast of Newfoundland, I found few haddock in NAFO Division 3L. Movement of haddock

along the east coast generally occurred in summer when surface water temperatures were highest and were thought to relate to movement patterns of capelin (*Mallotus villosus*), a common prey item for local haddock (Thompson 1939; May 1964). While haddock were found over a range of depths and temperatures in our study, they were primarily located at depths deeper and temperatures warmer than the median available. Bivariate analyses demonstrated that of the two habitat variables assessed, temperature was most influential in structuring haddock distribution. Across their range in the western Atlantic Ocean, haddock have been reported to exhibit differences in habitat preference. As on the Scotian Shelf (Scott 1982; Perry and Smith 1994; Smith et al. 1994), haddock off southern Newfoundland were found to be 'temperature-keepers', with individuals appearing to change depth in order to maintain similar temperature throughout the year. In contrast, Murawski and Finn (1988) indicated that haddock distributions on Georges Bank were more strongly related to depth than temperature, a difference which Perry and Smith (1994) postulated might have been due to the reduced range of depths sampled on Georges Bank (most full strata analyzed were <100 m) compared to the Scotian Shelf. It is possible, however, that strong depth associations among haddock on Georges Bank may relate not to differences in available depth, as proposed by Perry and Smith (1994), but rather greater access to optimal temperatures within this area. The latter hypothesis is supported by results of our study insofar as haddock distribution was driven primarily by temperature in all NAFO Divisions for which there were data, despite major differences in bathymetry among them (Table 2.1).

An additional aspect of this research was to explore potential differences in haddock habitat associations in relation to sex and maturity status. A number of gadoids including cod and haddock have been hypothesized to segregate sexually during the spawning season with mature males aggregating in areas where individuals possibly defend small territories and females only

venturing into these areas when ready to engage in courtship and spawning (Morgan and Trippel 1996; Hawkins and Amorim 2000; Nordeide and Folstad 2000; Dean et al. 2014). Contrary to expectation, I found little evidence for differences in habitat use between males and females or immature and mature fish. The observed pattern might relate to availability of suitable habitat in southern Newfoundland waters, particularly the predominance of cooler temperatures which may result in all individuals occupying similar areas regardless of sex or maturity status. An exception was the winter survey of NAFO Division 3P where immature males tended to occupy shallower and colder habitats than mature males. It is possible that fine-scale differences in habitat use exist but were not readily detected in the present study due to the inability of our methods to resolve variability at a scale finer than the area of a survey tow.

An important consideration in investigations of fish-habitat associations is the extent to which observed patterns might be influenced by environmental conditions or survey methodology. Multiple techniques exist for the quantification of fish habitat associations varying from relatively simple analyses using the mean and standard deviation of the habitat variable occupied (Murawski & Finn 1988) to using cumulative distribution functions (CDFs) based on catch data from random stratified surveys (Perry and Smith 1994; Smith et al. 1994; Swain et al. 1998). The methodology I opted to use (based on Perry and Smith 1994) to define fish-habitat associations which provides for rigorous comparisons based on the range of available environmental conditions during the survey. This analytical method accounts for survey design and available habitat conditions and does not require assumptions regarding the statistical distribution of fish catch or habitat variables (Perry and Smith 1994) which are often violated when undertaking parametric tests, such as general linear models, on complex surveys (Conover 1980; Rao and Thomas 1989). However, caution is warranted when comparing over time or

space given potential variability in the available environment, particularly when accompanied by changes to survey methodology. When habitat associations were assessed over multiple years as seen in our analysis of potential differences in relation to sex or maturity status, I attempted to control for these issues by examining all NAFO Divisions and seasons separately, as well as data collected before and after the introduction of the Campelen trawl. The change in survey gear in fall 1995 is particularly problematic as trawls used in previous years had wider meshes than the Campelen and thus small fish may have been underrepresented in earlier sampling (McCallum and Walsh 1996), which could confound analysis of habitat associations of mature and immature haddock through time. I observed a decrease in median depth used by haddock during the mid to late 1990s that broadly coincided with, and may have been attributable to, this change in gear. In some gadoids such as Atlantic cod, juveniles are distributed in shallower waters and exposed to colder conditions than their older counterparts (Clark and Green 1991). As a result, it is possible that this apparent shift in depth distribution was simply an artifact of increased catchability of juveniles following introduction of the Campelen trawl. However, in analyses that controlled for survey changes, I found little evidence to suggest consistent differences in habitat use between immature and mature individuals. In addition, while median depth used by haddock changed during this period, I did not detect a corresponding shift in median used temperature. Instead, analyses suggested that because of warmer environmental conditions, haddock may have been able to expand their distribution into shallower waters during recent years (Figure 2.7).

At the northern edge of their western Atlantic distribution, haddock off Newfoundland have historically exhibited reduced productivity compared to their southern counterparts (May 1964) hypothesized to be a result of decreased habitat availability imposed by cooler temperatures (Hodder 1963). Our analyses revealed that off southern Newfoundland, haddock were found

predominantly in temperatures of approximately 4-7 °C often representing some of the warmest waters available, particularly during the late 1980s and early 1990s when local environmental conditions were some of the coldest ever recorded (Figure 2.4; (Colbourne et al. 2014; DFO 2014c). Recent warming off Newfoundland and Labrador (Colbourne et al. 2014) has coincided with increases in local abundance of common resident species such as Atlantic cod (Rose and Rowe 2015; DFO 2015a, 2015b), as well as of some species typically associated with warmer water such as silver hake (*Merluccius bilinearis*; (Nye et al. 2011; DFO 2015a) or blue runner (*Caranx crysos*; (Devine and Fisher 2014). I found that the thermal environment typically occupied by haddock off Newfoundland has increased in availability over the last decade (Figure 2.4), particularly in NAFO Divisions 3LNO, and improved productivity of haddock might be predicted under warming scenarios (Hodder 1963; Fogarty et al. 2001; Rose 2005; Drinkwater 2006). Accordingly, above average biomass, abundance, and recruitment were apparent in the Grand Bank haddock stock during 2011 and 2012 (DFO 2014b). At the time of the haddock fishery collapse off Newfoundland, decreases in haddock abundance were attributed to poor survival of young fish (reviewed by Rose (2007). Indeed, abundance of haddock in the 1950s may have been unusually high due to warm temperatures favourable to recruitment during the 1940s and 1950s (Colbourne 2004). However, having removed many of the old/large haddock in the early years of the fishery (May 1964), it is likely that there may have been too few adults to produce a large number of young, particularly under deteriorating environmental conditions. The importance of older/larger individuals to population resilience of exploited marine fishes is a topic that has received increased attention of late (Marteinsdottir and Steinarsson 1998; Rowe and Hutchings 2003; Venturelli et al. 2009; Xu et al. 2013; Shelton et al. 2015) and measures

716 should be taken to promote and sustain broad size and age structure within haddock populations
717 moving forward.
718

2.6 Tables

Table 2.1. Mean, standard deviation, and relative error (standard deviation/mean) of the median bottom depth and temperature from habitat and haddock catch-weighted CDF curves calculated using available bottom trawl survey data of NAFO Divisions 3N (spring and fall), 3O (spring and fall), and 3P (winter and spring) during 1972-2013.

Habitat variable	NAFO Division	Season	Habitat			Used		
			Mean	Standard deviation	Relative error	Mean	Standard deviation	Relative error
Depth	3N	Spring	62.8	1.7	0.03	117.0	62.1	0.53
		Fall	62.7	1.7	0.03	65.0	25.7	0.39
	3O	Spring	80.5	2.1	0.03	122.1	48.2	0.39
		Fall	80.6	2.5	0.03	122.5	46.5	0.38
	3P	Winter	130.8	21.6	0.16	213.9	48.7	0.23
		Spring	143.5	8.3	0.06	167.2	81.7	0.49
Temperature	3N	Spring	1.2	0.7	0.60	3.0	1.5	0.50
		Fall	1.3	0.9	0.67	4.5	1.8	0.41
	3O	Spring	0.9	0.9	1.02	5.4	2.0	0.37
		Fall	1.4	0.9	0.68	4.7	2.0	0.43
	3P	Winter	0.7	1.4	1.92	5.1	1.7	0.34
		Spring	1.0	0.8	0.74	5.5	1.5	0.28

728 **Table 2.2.** P-values from the randomization test (equation 4) to examine differences in the
729 haddock catch-weighted cumulative frequency distributions and the unweighted cumulative
730 frequency distributions of habitat variables bottom depth and temperature during seasonal
731 bottom trawl surveys of NAFO Divisions 3N, 3O, and 3P for years in which data were available.
732 P-values represent the probability of obtaining, by chance, a test statistic as large or larger as
733 observed from the survey.

Habitat Variable	Year	3N		3O		3P	
		Spring	Fall	Spring	Fall	Winter	Spring
Depth	1972	--	--	--	--	<0.001	--
	1973	--	--	--	--	<0.001	--
	1974	--	--	--	--	<0.001	--
	1975	--	--	<0.01	--	--	--
	1976	<0.001	--	<0.01	--	0.01	--
	1977	<0.01	--	0.08	--	0.50	--
	1978	--	--	<0.001	--	0.02	--
	1979	0.09	--	0.04	--	<0.01	--
	1980	0.66	--	<0.001	--	0.02	--
	1981	0.21	--	0.61	--	0.12	--
	1982	<0.01	--	0.14	--	0.19	--
	1983	--	--	--	--	0.41	--
	1984	--	--	0.61	--	0.80	--
	1985	0.40	--	<0.001	--	0.01	--
	1986	0.91	--	<0.001	--	0.05	--
	1987	0.10	--	<0.01	--	<0.001	--
	1988	0.71	--	0.03	--	<0.01	--
	1989	0.08	--	<0.001	--	0.03	--
	1990	0.12	0.32	<0.001	<0.001	<0.001	--
	1991	0.02	0.65	<0.001	0.19	0.06	--
	1992	--	--	<0.001	<0.01	0.03	--
	1993	0.09	0.94	0.01	<0.001	--	<0.01
	1994	--	--	<0.001	<0.01	--	0.41
	1995	--	0.11	<0.01	0.02	--	0.47
	1996	0.60	--	<0.001	<0.001	--	0.45
	1997	0.19	0.13	0.05	<0.01	--	0.02
	1998	0.83	0.17	<0.01	0.01	--	0.85

	1999	0.79	0.38	0.24	<0.01	--	0.68
	2000	0.49	0.16	0.11	0.01	--	0.72
	2001	0.01	0.01	<0.01	0.54	--	0.67
	2002	0.08	0.55	0.18	0.29	--	0.70
	2003	--	0.25	0.06	0.01	--	0.07
	2004	0.56	0.11	0.08	0.14	--	0.88
	2005	0.21	0.86	0.02	0.92	--	0.44
	2006	--	0.46	--	0.08	--	--
	2007	0.38	0.33	0.46	0.38	--	0.73
	2008	0.70	0.17	0.55	0.54	--	0.79
	2009	0.33	0.02	0.50	0.28	--	0.85
	2010	0.62	0.02	0.11	<0.01	--	0.62
	2011	0.14	0.03	0.12	<0.01	--	0.49
	2012	0.54	0.19	0.30	<0.01	--	0.51
	2013	0.41	0.23	0.01	<0.01	--	0.54
Temperature	1972	--	--	--	--	<0.001	--
	1973	--	--	--	--	<0.001	--
	1974	--	--	--	--	--	--
	1975	<0.01	--	<0.001	--	--	--
	1976	0.88	--	<0.01	--	0.19	--
	1977	--	--	<0.001	--	<0.01	--
	1978	0.03	--	<0.01	--	<0.01	--
	1979	0.10	--	<0.001	--	<0.001	--
	1980	0.11	--	0.01	--	0.01	--
	1981	0.07	--	<0.001	--	0.05	--
	1982	--	--	--	--	0.13	--
	1983	--	--	--	--	0.08	--
	1984	0.03	--	<0.001	--	<0.001	--
	1985	0.20	--	<0.001	--	<0.001	--
	1986	<0.001	--	<0.001	--	<0.001	--
	1987	<0.001	--	<0.001	--	<0.01	--
	1988	0.05	--	<0.001	--	0.05	--
	1989	0.22	--	<0.001	--	<0.001	--
	1990	0.10	<0.01	<0.01	0.64	0.01	--
	1991	--	<0.01	<0.001	<0.001	<0.001	--
	1992	0.06	--	<0.001	<0.001	--	--
	1993	--	0.14	<0.001	<0.001	--	0.69
	1994	--	--	<0.001	0.01	--	<0.001
	1995	<0.001	0.21	<0.001	<0.01	--	<0.001

1996	0.79	0.28	0.09	<0.01	--	<0.01
1997	0.51	<0.001	<0.001	0.02	--	0.01
1998	0.12	<0.01	<0.01	0.03	--	0.02
1999	0.04	0.03	<0.01	<0.001	--	<0.01
2000	0.08	0.30	<0.001	0.65	--	0.27
2001	0.02	<0.01	<0.01	0.13	--	0.04
2002	--	<0.01	0.01	<0.001	--	<0.001
2003	0.08	<0.001	0.01	0.03	--	0.14
2004	0.73	0.01	<0.001	0.06	--	<0.001
2005	--	<0.001	--	0.03	--	0.01
2006	--	<0.01	--	0.08	--	--
2007	0.01	0.02	<0.01	0.01	--	0.06
2008	0.02	<0.001	0.03	<0.01	--	0.25
2009	0.02	<0.01	<0.001	0.21	--	0.09
2010	<0.01	<0.001	<0.01	<0.001	--	0.34
2011	0.02	<0.01	<0.001	<0.001	--	0.54
2012	0.29	0.06	<0.01	<0.001	--	<0.001
2013	<0.001	--	<0.001	<0.01	--	<0.01

734

735

736 **Table 2.3.** P-values from tests examining significance of differences in depth used by haddock
737 in relation to sex and maturity status (separating different NAFO Divisions, seasons, and survey
738 periods. Bold characters indicate statistically significant ($p \leq 0.05$) differences.

739

NAFO Division	Season	Years	Male vs. Female		Immature vs. Mature	
			Immature	Mature	Male	Female
3N	Spring	1975-1995	1.00	1.00	0.99	0.98
		1996-2013	1.00	0.83	0.13	0.07
	Fall	1990-1994	1.00	0.85	0.52	0.98
		1995-2013	1.00	0.97	0.92	0.57
3O	Spring	1975-1993	0.92	1.00	0.52	1.00
		1994-1995	1.00	0.93	1.00	0.74
		1996-2013	1.00	0.65	0.72	0.45
	Fall	1990-1993	1.00	0.99	0.61	0.97
		1994	1.00	1.00	1.00	1.00
		1995-2013	1.00	1.00	0.62	0.87
3P	Winter	1972-1993	0.39	1.00	**0.012**	0.20
	Spring	1994	1.00	1.00	0.92	0.74
		1995	0.99	1.00	0.99	0.94
		1996-2013	1.00	1.00	0.93	1.00

740

741 **Table 2.4.** P-values from tests examining significance of differences in temperature used by
742 haddock in relation to sex and maturity status (separating different NAFO Divisions, seasons,
743 and survey periods). Bold characters indicate statistically significant ($p \leq 0.05$) differences.

744

NAFO Division	Season	Years	Male vs. Female		Immature vs. Mature	
			Immature	Mature	Male	Female
3N	Spring	1975-1995	1.00	1.00	0.97	0.82
		1996-2013	1.00	0.79	0.26	0.17
	Fall	1990-1994	1.00	0.47	0.15	0.99
		1995-2013	0.53	0.97	0.19	0.67
3O	Spring	1975-1993	1.00	1.00	0.61	0.76
		1994-1995	1.00	1.00	0.94	0.94
		1996-2013	1.00	0.48	0.16	0.18
	Fall	1990-1993	0.97	0.98	0.63	0.50
		1994	1.00	1.00	1.00	0.99
		1995-2013	0.98	0.98	0.43	0.34
3P	Winter	1972-1993	0.29	0.97	**0.033**	0.51
	Spring	1994	1.00	1.00	0.91	1.00
		1995	0.99	1.00	0.94	0.91
		1996-2013	0.91	1.00	0.33	0.65

745

746 **Table 2.5.** P-values from the randomization test (equations 6, 7, and 8) for bivariate associations
747 between haddock catch and the hydrographic variables temperature and depth during seasonal
748 bottom trawl surveys of NAFO Divisions 3N, 3O, and 3P for years in which data were available.
749 P-values represent the probability of obtaining, by chance, a test statistic as large or larger as
750 observed from the survey. Bold characters indicate statistically significant ($p \leq 0.05$) habitat
751 associations.

752

Year	3N		3O		3P	
	Spring	Fall	Spring	Fall	Winter	Spring
1972	--	--	--	--	**<0.01**	--
1973	--	--	--	--	**<0.001**	--
1974	--	--	--	--	**<0.001**	--
1975	--	--	0.15	--	--	--
1976	**0.011**	--	**<0.01**	--	0.08	--
1977	**0.017**	--	**0.032**	--	0.66	--
1978	--	--	**<0.01**	--	**0.026**	--
1979	0.18	--	0.09	--	**<0.01**	--
1980	0.62	--	**<0.001**	--	**<0.01**	--
1981	0.65	--	0.28	--	0.22	--
1982	**0.027**	--	--	--	0.33	--
1983	--	--	--	--	0.38	--
1984	0.42	--	0.051	--	0.14	--
1985	0.78	--	**<0.001**	--	**<0.001**	--
1986	**0.018**	--	**<0.001**	--	**<0.01**	--

1987	**<0.01**	--	**<0.01**	--	**<0.001**	--
1988	--	--	**<0.01**	--	**<0.01**	--
1989	0.57	--	**<0.001**	--	--	--
1990	0.22	**0.037**	**<0.01**	**0.001**	**<0.001**	--
1991	--	0.07	0.49	0.51	--	--
1992	0.39	--	0.09	0.08	--	--
1993	--	0.84	0.09	**<0.001**	--	**<0.001**
1994	--	--	**0.012**	**0.020**	--	0.88
1995	--	0.27	**0.001**	0.09	--	**<0.001**
1996	0.31	--	**0.013**	**0.006**	--	**<0.001**
1997	0.82	0.43	0.23	**0.049**	--	**<0.01**
1998	0.93	**0.001**	**0.005**	0.27	--	**0.05**
1999	0.68	0.25	0.10	0.52	--	0.12
2000	0.38	0.33	0.08	**0.031**	--	**<0.01**
2001	0.09	0.25	**<0.01**	0.74	--	0.91
2002	0.29	0.06	0.06	0.52	--	0.08
2003	--	0.19	0.18	**0.022**	--	**0.038**
2004	0.39	**0.044**	0.26	0.42	--	0.71
2005	0.70	0.29	**<0.01**	0.46	--	**<0.01**
2006	--	0.14	--	0.27	--	--
2007	0.13	0.04	**0.036**	0.63	--	0.06
2008	0.21	0.29	0.14	0.13	--	0.24
2009	0.27	0.05	0.49	0.22	--	0.51
2010	0.34	0.15	**0.045**	0.09	--	0.75
2011	0.09	**0.049**	0.13	0.06	--	0.66

	2012	0.37	0.34	**0.013**	0.16	--	0.45
	2013	0.63	0.49	0.07	0.07	--	<**0.001**

753

754 **Table 2.6.** Depth and temperature values at the test statistic D (location of the maximum absolute difference between habitat and
755 catch-weighted cumulative distribution functions) for univariate ('Uni-'; Eq. 4) and bivariate ('Bi-'; Eq. 8) randomization tests
756 examining haddock habitat association patterns within seasonal bottom trawl surveys of NAFO Divisions 3N, 3O, and 3P. Cases in
757 which multiple results were obtained for the bivariate case are denoted by "Multiple".

758

		Spring				Fall				Winter			
Zone	Year	Depth		Temp		Depth		Temp		Depth		Temp	
		Uni-	Bi-	Uni-	Bi-	Uni-	Bi-	Uni-	Bi-	Uni-	Bi-	Uni-	Bi-
3N	1976	--	--	--	--	--	--	--	--	--	--	--	--
	1977	--	--	--	--	--	--	--	--	--	--	--	--
	1978	--	--	--	--	--	--	--	--	--	--	--	--
	1979	--	--	--	--	--	--	--	--	--	--	--	--
	1980	--	--	--	--	--	--	--	--	--	--	--	--
	1981	97	247	8.7	8.7	--	--	--	--	--	--	--	--
	1982	170	170	Multiple	3.1	--	--	--	--	--	--	--	--
	1983	--	--	--	--	--	--	--	--	--	--	--	--
	1984	177	333	7.8	7.8	--	--	--	--	--	--	--	--

1985	66	360	2.4	2.4	--	--	--	--	--	--	--	--
1986	71	365	7.2	7.2	--	--	--	--	--	--	--	--
1987	115	108	0.4	Multiple	--	--	--	--	--	--	--	--
1988	--	--	--	--	--	--	--	--	--	--	--	--
1989	66	66	2.4	3.2	--	--	--	--	--	--	--	--
1990	64	320	1.1	1.1	--	--	--	--	--	--	--	--
1991	65	Multiple	1.6	1.6	--	--	--	--	--	--	--	--
1992	75	Multiple	2.4	2.4	--	--	--	--	--	--	--	--
1993	206	--	4.2	--	--	--	--	--	--	--	--	--
1994	105	105	3.5	7.5	--	--	--	--	--	--	--	--
1995	310	310	1.6	Multiple	56	291	6.2	6.2	--	--	--	--
1996	--	--	--	--	42	638	4	4	--	--	--	--
1997	305	Multiple	2.5	2.5	--	--	--	--	--	--	--	--
1998	--	--	--	--	64	Multiple	2.1	2.1	--	--	--	--
1999	--	--	--	--	--	--	--	--	--	--	--	--
2000	--	--	--	--	40	210	5.6	5.6	--	--	--	--
2001	59	665	3.4	3.4	--	--	--	--	--	--	--	--
2002	127	127	0.9	Multiple	59	59	3.1	6.6	--	--	--	--

	2003	65	Multiple	2.7	2.7	50	1447	6.2	6.2	--	--	--	--
	2005	51	Multiple	3.2	3.2	61	664	6	6	--	--	--	--
	2006	61	Multiple	3.2	3.2	63	63	2.5	4.5	--	--	--	--
	2007	219	237	3.8	Multiple	57	57	1	6,6.1	--	--	--	--
	2008	45	641	3.7	3.7	64	1429	3.4	3.4	--	--	--	--
	2009	--	--	--	--	65	Multiple	1.8	1.8	--	--	--	--
	2010	60	Multiple	3.4	3.4	61	Multiple	3.7	3.7	--	--	--	--
	2011	69	69	1.4	Multiple	61	1445	3.9	3.9	--	--	--	--
	2012	--	--	--	--	56	Multiple	2.8	2.8	--	--	--	--
	2013	58	Multiple	2.9	2.9	62	1419	3.7	3.7	--	--	--	--
3O	1975	99	99	1.7	Multiple	--	--	--	--	--	--	--	--
	1976	91	362	7.1	7.1	--	--	--	--	--	--	--	--
	1977	88	143	0.7	0.7	--	--	--	--	--	--	--	--
	1978	116	Multiple	4.7	4.7	--	--	--	--	--	--	--	--
	1979	93	137	5.8	5.8	--	--	--	--	--	--	--	--
	1980	121	92	3	Multiple	--	--	--	--	--	--	--	--
	1981	113	Multiple	2.7	2.7	--	--	--	--	--	--	--	--
	1982	91	--	2.4	--	--	--	--	--	--	--	--	--

1983	--	--	--	--	--	--	--	--	--	--	--	--
1984	91	128	2.8	2.8	--	--	--	--	--	--	--	--
1985	72	Multiple	0.8	0.8	--	--	--	--	--	--	--	--
1986	126	246	3.9	7.2	--	--	--	--	--	--	--	--
1987	198	Multiple	2.5	2.5	--	--	--	--	--	--	--	--
1988	93	335	7.9	7.9	--	--	--	--	--	--	--	--
1989	94	123	1.7	1.7	--	--	--	--	--	--	--	--
1990	96	126	2.6	Multiple	130	130	1.9	7.1	--	--	--	--
1991	133	130	1.1	Multiple	69	69, 70	1.3	1.5	--	--	--	--
1992	130	Multiple	1.8	1.8	129	Multiple	4.3	4.3	--	--	--	--
1993	139	620	4.7	4.7	145	676	4.8	4.8	--	--	--	--
1994	110	132	2.3	Multiple	124	696	4.2	4.2	--	--	--	--
1995	140	149	3.4	3.4	104	139	3.6	3.6	--	--	--	--
1996	89	685	4.4	4.4	139	212, 213	6.4	7.8	--	--	--	--
1997	93	140	2	Multiple	99	Multiple	1.2	1.2	--	--	--	--
1998	227	616	5.1	5.1	84	84	2.8	Multiple	--	--	--	--
1999	98	679	5.8	5.8	95	95	3.2	5.8	--	--	--	--

	2000	83	118	3.4	3.4	114	1424	4.7	4.7	--	--	--	--
	2001	97	Multiple	2	2	70	74	1.1	Multiple	--	--	--	--
	2002	89	Multiple	3.2	3.2	80	112	1.8	1.8	--	--	--	--
	2003	86	Multiple	0.8	0.8	101	1382	4.8	4.8	--	--	--	--
	2004	84	636	4.7	4.7	66	142	3	3	--	--	--	--
	2005	99	719	5.2	5.2	99	Multiple	2.8	2.8	--	--	--	--
	2006	--	--	--	--	96	97103	2.5	2.5	--	--	--	--
	2007	83	719	4.6	4.6	110	1410	4.8	4.8	--	--	--	--
	2008	76	Multiple	2.8	2.8	86	93	1	2	--	--	--	--
	2009	85	674	5.4	5.4	91	Multiple	1.9	1.9	--	--	--	--
	2010	96	673	5.5	5.5	95	95	3.5	Multiple	--	--	--	--
	2011	80	128	4.5	4.5	99	Multiple	3.7	3.7	--	--	--	--
	2012	97	117	2.4	2.4	94	117	4.1	Multiple	--	--	--	--
	2013	90	129	5.8	4	118	Multiple	4.7	3.1	--	--	--	--
3P	1972	--	--	--	--	--	--	--	--	159	159	2.5	4.8
	1973	--	--	--	--	--	--	--	--	155	Multiple	2.3	2.3
	1974	--	--	--	--	--	--	--	--	141	141	1.4	Multiple
	1975	--	--	--	--	--	--	--	--	--	--	--	--

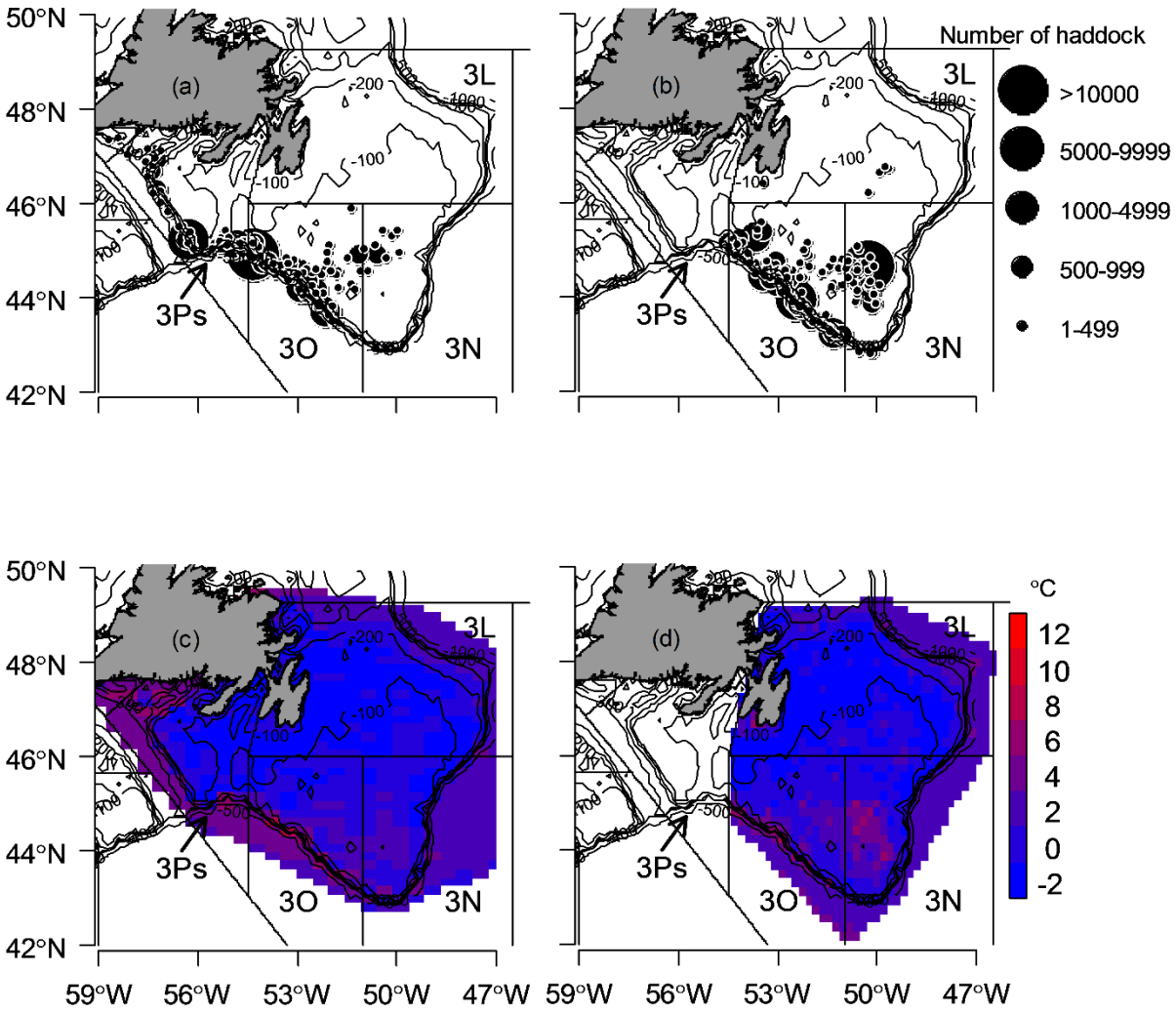
1976	--	--	--	--	--	--	--	--	146	Multiple	2.4	2.4
1977	--	--	--	--	--	--	--	--	123	Multiple	1.1	1.1
1978	--	--	--	--	--	--	--	--	165	Multiple	2.4	2.9
1979	--	--	--	--	--	--	--	--	172	466	6.6	6.6
1980	--	--	--	--	--	--	--	--	154	549	5	5
1981	--	--	--	--	--	--	--	--	157	499	6.7	6.7
1982	--	--	--	--	--	--	--	--	50	162	-0.7	-0.7
1983	--	--	--	--	--	--	--	--	140	663	4.9	4.9
1984	--	--	--	--	--	--	--	--	172	171	1.5	2.5
1985	--	--	--	--	--	--	--	--	208	628	6.7	6.7
1986	--	--	--	--	--	--	--	--	166	598	6.5	6.5
1987	--	--	--	--	--	--	--	--	156	Multiple	4	4
1988	--	--	--	--	--	--	--	--	155	155	0.8	Multiple
1989	--	--	--	--	--	--	--	--	178	--	5	--
1990	--	--	--	--	--	--	--	--	209	497	5.3	5.3
1991	--	--	--	--	--	--	--	--	208	--	4.7	--
1992	--	--	--	--	--	--	--	--	200	--	5.5	--
1993	178	635	6.2	6.2	--	--	--	--	--	--	--	--

1994	412	412	4.1	7.6	--	--	--	--	--	--	--	--
1995	209	613	6	6	--	--	--	--	--	--	--	--
1996	124	613	5.9	5.9	--	--	--	--	--	--	--	--
1997	154	637	2.7	6.1	--	--	--	--	--	--	--	--
1998	102	670	6.2	6.2	--	--	--	--	--	--	--	--
1999	162	870	5	5	--	--	--	--	--	--	--	--
2000	98	608	6.7	6.7	--	--	--	--	--	--	--	--
2001	140	Multiple	1.9	1.9	--	--	--	--	--	--	--	--
2002	136	625	6.2	6.2	--	--	--	--	--	--	--	--
2003	203	675	5.1	5.1	--	--	--	--	--	--	--	--
2004	138	591	5	5	--	--	--	--	--	--	--	--
2005	116	658	5.3	5.3	--	--	--	--	--	--	--	--
2006	202	--	--	--	--	--	--	--	--	--	--	--
2007	100	601	6.4	6.4	--	--	--	--	--	--	--	--
2008	130	Multiple	2.9	2.9	--	--	--	--	--	--	--	--
2009	120	678	5	5	--	--	--	--	--	--	--	--
2010	136	Multiple	2.5	2.6	--	--	--	--	--	--	--	--
2011	157	622	3.3	6.2	--	--	--	--	--	--	--	--

2012	112	Multiple	0.7	0.8	--	--	--	--	--	--	--	--
2013	159	608	5.5	5.5	--	--	--	--	--	--	--	--

759

760 **2.7 Figures**



761

762 **Figure 2.1** Waters off Newfoundland showing NAFO Divisions, trawl locations with
763 scaling symbols to denote number of haddock caught per set (a and b), and bottom
764 temperatures (c and d) during surveys conducted in winter/spring (a and c) and fall (b and
765 d) based on available data spanning 1972-2013.

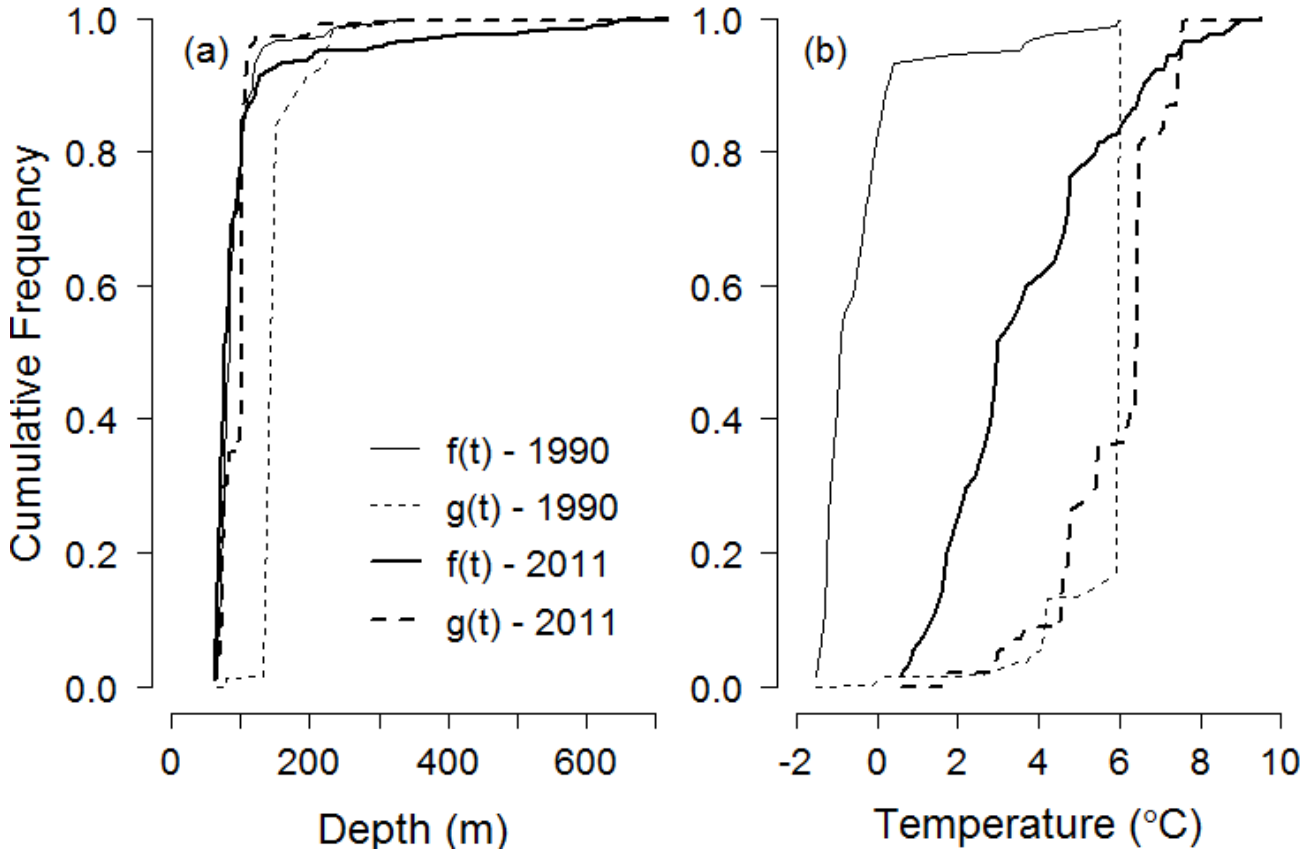


Figure 2.2. Habitat (f(t); Eq. 1; solid lines) and haddock catch-weighted (g(t); Eq. 2; dashed lines) cumulative distribution functions for the habitat variables bottom depth (a) and temperature (b) during the spring bottom trawl survey of NAFO Division 3O in 1990 (thin lines) and 2011 (thick lines).

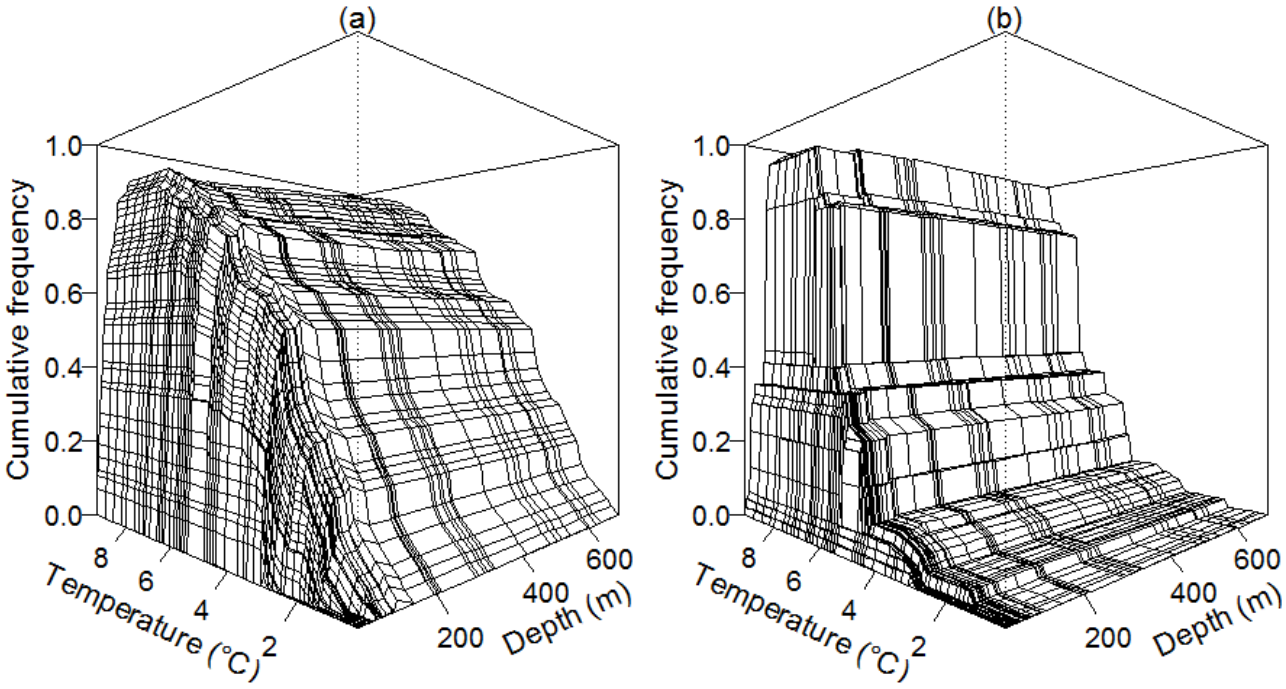
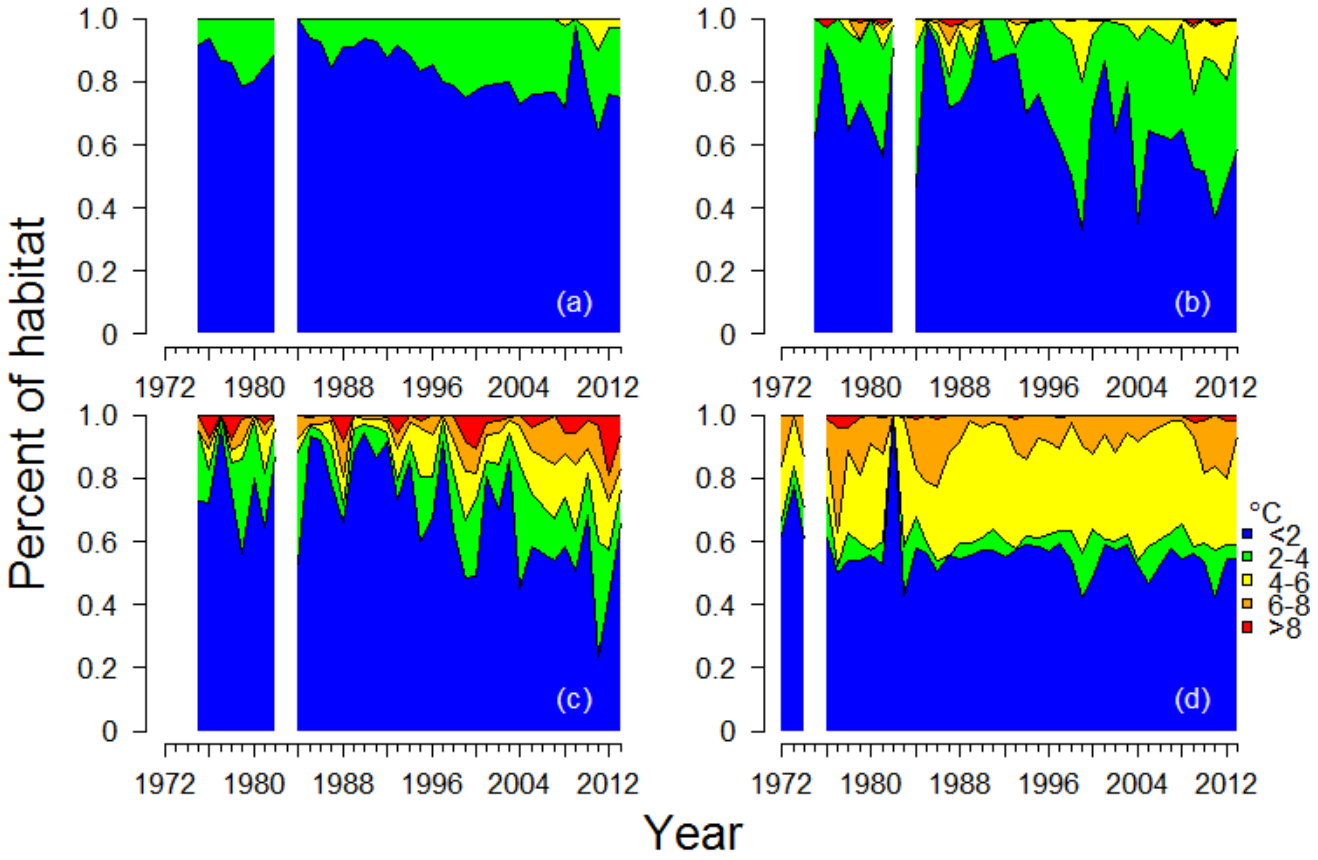


Figure 2.3. Bivariate (depth and temperature) cumulative frequency surfaces for habitat available (a) and habitat used by haddock (b) during the spring bottom trawl survey of NAFO Division 3O in 2011. Note that back walls of depth and temperature axes represent the same cumulative distribution functions as calculated for univariate cases (Eq. 1 and 2).

784



785

786 **Figure 2.4.** Percent of survey area covered by various water temperatures based on
787 bottom temperature measured as part of annual winter/spring bottom trawl surveys of
788 NAFO Divisions 3L (a), 3N (b), 3O (c), and 3P (d) during 1972-2013. Percent coverage
789 was calculated using design weighted area of occupancy for various thermal ranges (Eq.
790 9).

791

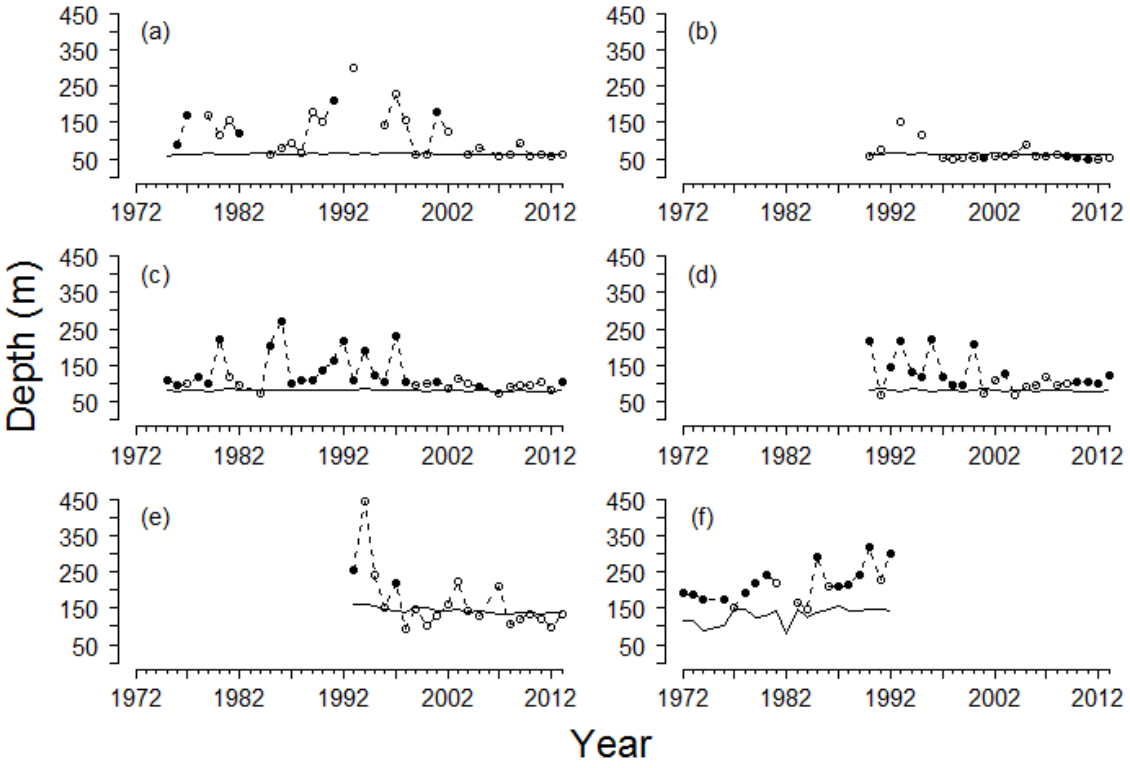


Figure 2.5. Median depth available (solid line) and median depth used (circles and dashed line) by haddock through time for spring (a, c, and e), fall (b and d), and winter (f) bottom trawl surveys in NAFO Divisions 3N (a and b), 3O (c and d), and 3P (e and f). Closed circles indicate statistically significant ($p \leq 0.05$) habitat associations for the specified year.

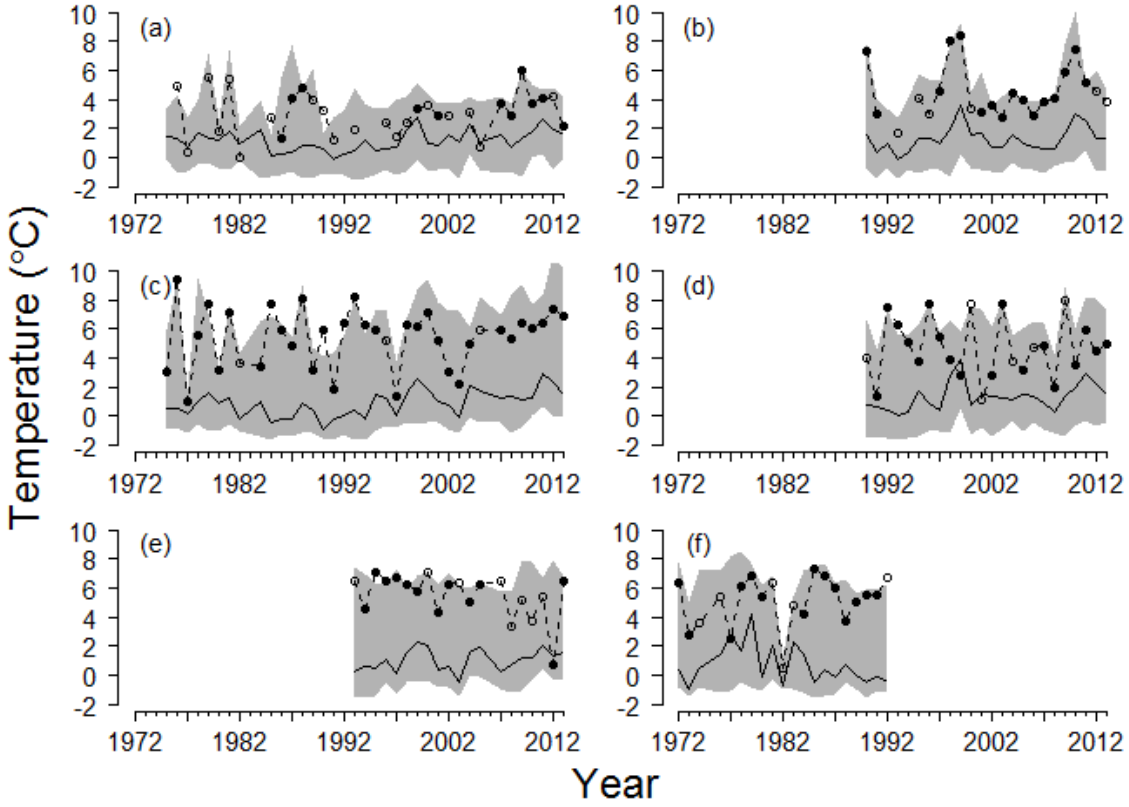
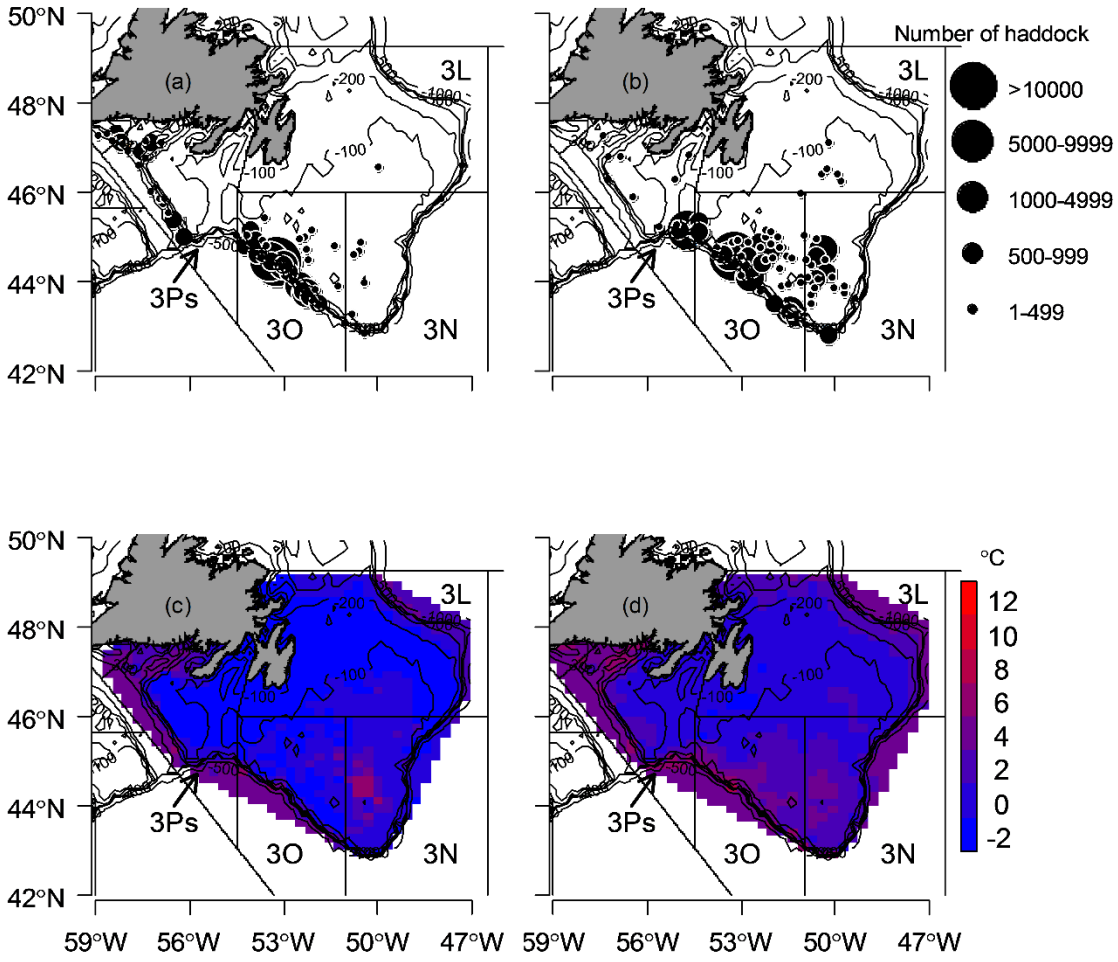


Figure 2.6. Median temperature available (solid line) and median temperature used (circles and dashed line) by haddock through time for spring (a, c, and e), fall (b and d), and winter (f) bottom trawl surveys in NAFO Divisions 3N (a and b), 3O (c and d), and 3P (e and f). Grey polygons represent 95% confidence limits for available habitat and closed circles indicate statistically significant ($p \leq 0.05$) habitat associations for the specified year.



807

808 **Figure 2.7.** Waters off Newfoundland showing NAFO Divisions, trawl locations with
809 scaling symbols to denote number of haddock caught per set (a and b), and bottom
810 temperatures (c and d) during surveys conducted in 1990-1993 (a and c; 'cold years') and
811 2010-2013 (b and d; 'warm years') based on available data.

812

813

Summary

Changes to life history and behaviour of a species have coincided with the collapse of many stocks (Ricker 1981; Rijnsdorp 1993; Trippel et al. 1997; Olsen et al. 2004; Swain et al. 2007). The collapse of whole stocks, like the haddock stocks in Newfoundland waters, highlights the need to understand how these changes affect stock structure and functioning and their role in sustainable management of fisheries.

Decreases in size and growth due to prolonged size-selective fishing pressure as well the increases in growth or maturity that might be expected from a population experiencing a release from density-dependent growth restrictions have not been observed in Newfoundland haddock stocks. This lack of growth and maturity changes observed in Newfoundland haddock through the last several decades add an additional complexity to what is currently understood about over-exploited fish stocks.

Although density-dependence was not examined in this study, it is conceivable that density-dependent effects could be contributing to the persistently low abundance of haddock in Newfoundland waters. Although paradoxical, this hypothesis may be grounded in data. As discussed in Chapter 2, haddock preferentially occupy a temperature range of ~4-8°C. Throughout much of the study period, and particularly in the late 1980s and the 1990s, these temperatures were not readily available in spring or winter outside of the narrow shelf slope (~200-300 m) and as such haddock were crowded into these areas. Density-dependent effects may have indeed hampered growth of the population but not of the individuals based due to limited habitat availability by causing low recruitment and poor productivity.

Although haddock recruitment in Newfoundland waters is variable, it tends to be cyclical with a moderate year class occurring every 3-5 years and exceptional year classes being much more infrequent. This cyclical pattern was disrupted when the fishery began and the largest, oldest fish were removed from the population therefore decreasing the total reproductive output of the stocks, meaning fewer fish could be recruited. This trend continued until the 1960s, when catch rates were depleted well below the level required for an economically feasible fishery. The next large year classes appeared in 1982 (likely the 1979 year class) and 1984-1985 (likely the 1981-1982 year classes) and seem to coincide with a warming phase in the Atlantic Multidecadal Oscillation. These year classes would have likely spawned more strong year classes, but contraction of available habitat due to rapid decreases in sea temperatures in the late 1980s and 1990s coupled with continued removals in the form of by-catch caused recruitment to decrease again. This decreased recruitment has continued to persist although signs of improved stock structure and increased abundance coupled with increasing availability of preferred thermal habitat may indicate another strong year class in the coming years.

Re-establishment of a sustainable fishery for Newfoundland haddock will require quantitative investigations into the recruitment dynamics of these stocks as well as studies into reproductive potential of haddock in Newfoundland waters. Additionally, information on the consequences of haddock by-catch in these areas would help to improve stock status.

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